© 2016 Blackwell Verlag GmbH

ISSN 0175-8659





Received: August 12, 2016 Accepted: October 19, 2016 doi: 10.1111/jai.13240

# Status of Lake Sturgeon (Acipenser fulvescens Rafinesque 1817) in North America

By R. M. Bruch<sup>1</sup>, T. J. Haxton<sup>2</sup>, R. Koenigs<sup>1</sup>, A. Welsh<sup>3</sup> and S. J. Kerr<sup>2</sup>

<sup>1</sup>Wisconsin Department of Natural Resources, Oshkosh, WI, USA; <sup>2</sup>Ontario Ministry of Natural Resources and Forestry, Peterborough, ON, Canada; <sup>3</sup>School of Natural Resources, West Virginia University, Morgantown, WV, USA

#### **Summary**

Lake Sturgeon is a potamodromous, fluvial-dependent species from the family Acipenseridae, and one of the largest freshwater fishes within its North American range extending to the Great lakes, Mississippi River, and Hudson Bay drainages. Like almost all other sturgeon species, Lake Sturgeon populations throughout its range suffered mass declines or extirpation in the late 1800s into the early 1900s, due to extensive overexploitation and habitat loss and alteration. However, Lake Sturgeon are still present in low to high densities throughout their native range due primarily to factors including: the species long life span and resiliency, the remote location of many northern populations, long-term pro-active management programs effectively controlling exploitation, improved habitat and water-quality conditions, and recovery programs that have been in effect since the late 1970s. Recovery programs initiated in the late 1970s are now just beginning to show signs of natural recruitment from populations re-built with stocked fish. Large sustainable recreational Lake Sturgeon fisheries with annual harvests of up to 45 000 kg and a commercial fishery with an annual harvest of up to 80 000 kg still exist and are maintained for Lake Sturgeon due primarily to rigid regulations, harvest controls, enforcement, and user involvement. The prognosis for the species is generally good, although habitat loss and maintaining public interest in the species management and recovery continue to be the greatest threats to local and regional populations. Hydropower development, especially in the northern part of the species' range, is especially challenging due to the potential negative impact this type of development can have on a long migrating fish like Lake Sturgeon. Advances in understanding Lake Sturgeon life history, habitat requirements, and distribution within and among water systems has strongly indicated that dams and Lake Sturgeon can coexist, if the correct planning and necessary mitigative techniques are employed at each site on a case-by-case basis.

# Taxonomy

Acipenser fulvescens Rafinesque 1817 AFS English common name: Lake Sturgeon Quebec French vernacular name: esturgeon jaune Other vernacular names: rock sturgeon, common sturgeon, rubbernose The species Lake Sturgeon (LS) had been assigned at least 17 different scientific names during the 19th and 20th centuries due to the variation in color and shape displayed by the different life stages and populations (Scott and Crossman, 1973). Eventually LS was recognized as one species with the scientific designation *Acipenser fulvescens* (fulvescens = yellowish or tawny) originally proposed by Constantine Samuel Rafinesque (1783–1840). The common name Lake Sturgeon was given due to the abundance of the species in the Great Lakes (Harkness and Dymond, 1961).

#### Phylogeny

Fossil evidence indicates that sturgeons evolved as a phyletic group approximately 200 million years ago (Bemis et al., 1997). Although Acipenseriformes is generally agreed by taxonomists to be a monophyletic group, the phylogenetic relationships of the genus *Acipenser* has been questioned with suggestions that the members of the genus do not share a single synapomorphic molecular character indicating possible multiple evolutionary lineages (Birstein et al., 2002). In any event, members of the genus share numerous common morphological features, although LS is the only species in the genus that naturally completes all of its lifecycle in freshwater (i.e. potamodromous).

#### Distribution and general abundance

LS have one of the widest natural distributions of all freshwater fish in North America (Harkness and Dymond, 1961) and were historically found in the Mississippi, Great Lakes–St.Lawrence River, and Hudson Bay drainages (Fig. 1). Their native range extends from the Hudson Bay southward to the southern border of Arkansas and eastward to the Tennessee River in Alabama, and from the foothills of the Rocky Mountains in Alberta to the estuary of the St. Lawrence River approximately 110 km east of Quebec City (Harkness and Dymond, 1961; Scott and Crossman, 1973).

Historically, LS were considered abundant (Harkness and Dymond, 1961; Tody, 1974). Commercial harvest records from the Great Lakes provide some insight into historical abundance of LS with documented annual harvest of up to one million kg from a single lake (Harkness and Dymond, 1961; Auer, 1999a; OMNR, 2009). Using the commercial

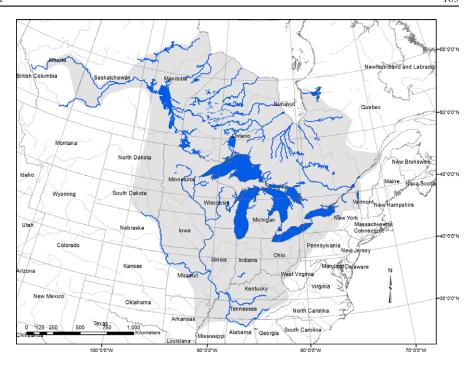


Fig. 1. LS historic range (shaded area) (adapted from Harkness and Dymond, 1961), and present distribution (blue colored waters) in North America

harvest data for each of the Great Lakes, initial LS biomass was estimated to range from 313 000 kg in Lake Superior to 6 473 000 kg in Lake Erie (Table 1; Haxton et al., 2014a). However, LS abundance has been greatly reduced in the Great Lakes, and throughout much of their range, (Hubbs and Lagler, 1947) to the extreme low levels where Great Lakes populations are now estimated to be <1% of historical numbers (Hay-Chmielewski and Whelan, 2003). Across their range, LS are currently considered extirpated in four states, endangered in 11 states and provinces, threatened in four states and provinces (considered threatened in only a portion of Ontario), and of special concern in four states and provinces (Table 2). The International Union on the Conservation of Nature (IUCN; www.iucnred-list.org), however, globally lists the status of LS as least concern. The largest LS populations remaining are believed to exist in the St. Lawrence River east of Montreal in Canada (Mailhot et al., 2011), the Lake of Woods/Rainy River population in the

Table 1 Estimated historical biomass (kg) with variation of lake sturgeon in the Great Lakes based on Markov-chain Monte Carlo estimates using the surplus-production model (Haxton et al. 2014a)

Waterbody	Estimated historical biomass (1000s kg)	Standard deviation	Lower 95% CI	Upper 95% CI
Lake Superior	314	99	241	590
Lake Michigan	3909	1224	3017	7148
Lake Huron	1929	662	1507	3532
Lake St. Clair	2054	564	1609	3644
Lake Erie	6473	2133	5028	11470
Lake Ontario	1044	321	805	1916

United States (Heinrich and Friday, 2014), the Winnebago System in United States (Bruch, 1999), and St. Clair Lake within the Great Lakes (Peterson et al., 2007).

As such, the present range of LS is somewhat retracted from the historical distribution with the species being either absent or sparsely populated in some areas, especially in the far southern and southeastern portions of the range. Several rivers flowing into Hudson Bay represent the last unfragmented habitat (Dynesius and Nilsson, 1994; Nilsson et al., 2005; OMNR, 2009) where LS exist. The remoteness of these populations likely prevented them from the excessive harvests of the late 1800s and early 1900s as fishermen moved inland to tributaries and rivers following population crashes in the Great Lakes (Bemis and Findeis, 1994). Therefore, these populations could be important as they provide the only glimpse into the dynamics of 'pristine' populations.

# **Population metrics**

# Current abundance

Populations of LS that currently exist throughout the original range including native as well as new populations that are being restored, have adult abundance levels ranging from dozens of individuals, e.g., many Great Lakes tributaries (Holey et al., 2000) to tens of thousands of individuals, e.g., Winnebago System, WI (Bruch, 1999), Lake of the Woods/Rainy River (Heinrich and Friday, 2014), and lower St. Lawrence River (Dumont et al., 1987) (Fig. 1). The general trend in abundance seems to be positive for LS throughout its range in North America due to increased efforts to improve habitat and water quality, effectively manage or eliminate/minimize exploitation impacts, and improve and/or restore populations through stocking and transfers.

Table 2 Jurisdictional status of lake sturgeon across states and provinces

State/Province	Country	Designation
Alabama	United States	Extirpated
Alberta	Canada	Endangered <sup>1</sup>
Arkansas	United States	Extirpated
Georgia	United States	Extirpated
Illinois	United States	Endangered
Iowa	United States	Endangered
Kentucky	United States	Endangered
Manitoba	Canada	Endangered <sup>1</sup>
Michigan	United States	Threatened
Minnesota	United States	Special Concern
Missouri	United States	Endangered
Nebraska	United States	Threatened
New York	United States	Threatened
North Carolina	United States	Special Concern
North Dakota	United States	Unknown
Ohio	United States	Endangered
Ontario		
Hudson Bay – James Bay population	Canada	Special Concern
Great Lakes-St. Lawrence population		Threatened <sup>2</sup>
Northwestern Ontario population		Threatened <sup>2</sup>
Pennsylvania	United States	Endangered
Quebec	Canada	At Risk
Saskatchewan	Canada	Endangered <sup>2</sup>
Tennessee	United States	Endangered
Vermont	United States	Endangered
West Virginia	United States	Extirpated
Wisconsin	United States	Special Concern

<sup>&</sup>lt;sup>1</sup>Proposed status by Committee on the Status of Endangered Species in Canada.

# Age and growth

LS, like nearly all other sturgeon species, are known to be slow growing (Harkness, 1923; Schneberger and Woodbury, 1946; Cuerrier and Roussow, 1951; Probst and Cooper, 1954; Priegel and Wirth, 1971; Folz and Meyers, 1985; Rossiter et al., 1995; Bruch, 1999), late maturing (Winemiller and Rose, 1992) periodic life history strategists. While age is one of the most important datum collected on a fish for management purposes, accurate and precise ages are often difficult to collect for most fish species, especially for a long lived cartilaginous fish like LS. Sturgeon have a limited number of bony structures that can be used to estimate age of an individual with counting annual growth increments observed from cross sections of pectoral fin spines being the most commonly applied method. Accuracy of ages estimated from pectoral fin ray spines has been questioned for many years (Brennen and Caillet, 1989; Rien and Beamesderfer, 1994; Paragamian and Beamesderfer, 2003; Bruch et al., 2009). Rossiter et al. (1995) corroborated age estimates for LS by observing that the difference in age estimates derived from pectoral fin spines matched the years at liberty between capture events. However, this is not true validation as the captured fish were not of known-age and the study did not sample fish from the full array of potential ages. Bruch et al.

(2009) reported a consistent underestimation error for LS over the age of 14 and developed a correction factor to assign age estimates potentially closer to the true age of the fish for the Winnebago system: True Age =  $1.35073 \times (Est Age^{0.9606})$ .

Otoliths have been used and validated for LS (Bruch et al., 2009), but these structures are primarily composed of Vaterite (a thermodynamically unstable polymorph of calcium carbonate; all otoliths are comprised of stable Calcite, metastable Aragonite and/or unstable Vaterite) which make them difficult to work with. Further, fish need to be sacrificed to collect otoliths, which significantly limits their use in management of most LS populations.

The oldest LS age on record was a 94.3 kg (208 lb) fish taken from Lake of Woods, Ontario in 1953 and estimated to be 154 years of age (Online at: http://www.dfo-mpo.gc.ca/ species-especes/species-especes/sturgeon6-esturgeon-eng.htm, accessed 10 January 2016). While no one knows for certain whether this fish was actually 154 years old, long term tagging studies have demonstrated that LS can live a very long time and that ages of 150 plus years are not unreasonable. LS biologists will eventually be able to discern the true maximum age of LS given the significant increases in tagging studies, especially studies with low or no-loss tags such as PIT tags in use since the 1990s. Also, almost all populations have been negatively impacted by exploitation and other factors before, during and after the time LS have been scientifically and systematically examined for age (since the 1940s), which would tend to reduce or eliminate the largest and oldest individuals in each population. This phenomenon would result in most LS populations being comprised generally of younger animals, in turn biasing any estimate of maximum age obtained from empirical data. Given the increases in protections and pro-active management that many LS populations in North America now enjoy, along with what we understand as the innate life history of the species, LS may be on track to exhibit their true growth and longevity potential before the year 2100.

Growth in length for LS is considered rapid for the first 10-15 years of life followed by relatively slow growth at the onset of puberty and eventual sexual maturation as energy is directed to gonadal development from somatic growth (Harkness, 1923; Magnin, 1966; Scott and Crossman, 1973; Bruch, 2008). Growth in length for both sexes is similar in pre-pubescence, but becomes dimorphic in post-pubescence with females exhibiting faster growth rates and attaining larger sizes as adults (Bruch, 1999, 2008). Estimated length at age data (using corrected age data) for the Winnebago System indicate that both males and females reach 120 cm at age 20 with dimorphic growth resulting in males averaging 168 cm and females 187 cm at age 65 (Fig. 2; Table 3). Growth in LS varies among populations with exclusively lotic populations often exhibiting slower growth (Priegel, 1973) and populations with access to lentic feeding grounds exhibiting faster growth (Bruch, 2008). Growth also varies significantly within populations and within individual fish (Bruch, 2008; Haxton and Findlay, 2008), especially for mature males which typically grow very little following maturation (Bruch, 2008; Heinrich and Friday, 2014). This slow

<sup>&</sup>lt;sup>2</sup>Ontario Endangered Species Act.

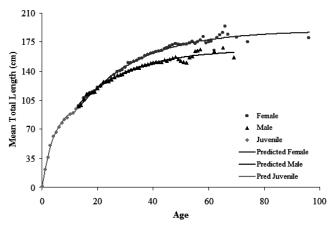


Fig. 2. Mean length at age of LS, larvae and juveniles age 0–12, males age 13–69 and females age 13–96 in the Winnebago System, Wisconsin, 1953–2007. "Predicted" shows von Bertalanffy curves fit to each group. Original pectoral fins spine ages >14 corrected with TrueAge = EstAge<sup>1.054796</sup> (from Bruch 2008).

Table 3
Estimated mean total length (cm) of Winnebago System, WI male and female LS using corrected age data (Bruch et al., 2009; and R. Koenigs, WI Dept. of Natural Resources, Oshkosh, WI, unpubl. data)

Age	Male	Female
Hatching	0.9	0.9
Emergence	1.8	1.8
1	22	22
2	36	36
3	51	51
4	62	62
5	66	66
10	88	88
15	107	107
20	120	120
25	130	132
35	144	155
45	152	168
55	164	173
65	168	187

to no-growth pattern emphasizes the need to minimize measurement error when measuring sturgeon lengths. Historically spawning and harvested LS on the Winnebago System were measured to the nearest 0.5 inch (1.27 cm) which, given the low mean annual growth increments, resulted in measurement error that could have been avoided had the fish been measured more accurately.

# Weight and length

The greatest weight reported for LS was a 180 kg (396 lb) fish captured in the Roseau River, Manitoba (Manitoba Hydro, 2014). A review of recreationally caught LS from states and provinces in the upper Midwest US and Canada show a 122.5 kg angler-caught fish in Saskatchewan in 1962 and a 93.3 kg fish speared in Wisconsin in 2010 (Table 4).

Most LS reported in scientific literature, as well as in angler reports, rarely exceed 50 kg – another possible symptom of past overexploitation of the larger fish in many populations and/or a sign of younger average ages in the stock due to recovery taking place.

The weight-length relationships of LS vary depending upon the sex, maturity, and gonadal condition of the individual fish being sampled. Further, season and location of the population (lentic, lotic, north, south) can strongly influence length-weight relationships. For these reasons, there are dozens of weight-length relationships reported in the literature for LS (e.g. Cuerrier and Roussow, 1951; Probst and Cooper, 1954; Sunde, 1961; Royer et al., 1968; Priegel, 1973; Threader and Brousseau, 1986; Dumont et al., 1987; Nowak and Jessop, 1987; Sandilands, 1987; Fortin et al., 1992; McDonald, 1998; Jackson et al., 2002; Craig et al., 2005; Smith and Baker, 2005; Adams et al., 2006; Bruch, 2008; Lallaman et al., 2008; Bruch et al., 2011).

Weight and length are typically the data most consistently collected by fisheries biologists in field assessments. Given the serious measurement error in determining sturgeon lengths, and the inherent error with estimating age, weight is likely the one metric that can be collected relatively consistently and accurately. The problems with weight data stem from variation in weight at a certain length caused by factors mentioned earlier (i.e., sex, maturity, latitude, location). Bruch et al. (2011) examined 63 W-L relationships of LS from 43 populations throughout their range and recommended that LS W-L relationships should be developed using data from fish representing different growth stanzas, as well as split by sex and stage of maturity when possible. Further, Bruch et al. (2011) recommended applying a new metric, the Modified Form Factor (mFF), as a quick and simple metric to compare mean condition among sturgeon stocks or between components within a stock. The mFF is represented by the equation:

$$mFF = 1000 \times (10^{(Log_{10}\alpha - (-2.129 \times (\beta - 3)))}).$$

This metric can be used as a tool to evaluate the condition of a LS population, or groups within the population, by comparing their modified form factors to those derived from other LS populations whose weight—length relationships have already been described. Additionally, the condition of LS populations can be compared between regions using a Student's *t*-test to assess for significance. For example, you could compare two sets of modified form factors calculated from spawning males sampled in Wisconsin to spawning males sampled from Ontario stocks.

### Fork length-total length relationship

Fork length to total length relationships were developed for LS from the Winnebago System in Wisconsin based on 388 paired measurements (range: 102-185 cm TL) as  $FL = (0.966663 \times TL) - 6.5506$  (R. M. Bruch, WDNR, unpubl. data). Comparatively, data collected from 33 paired measurements (range: 32-156 cm TL) from the lower Niagara River, New York, reported a fork length to total length

Table 4
Recreational fishing LS record fish for upper Midwest US and Canada (Online at: http://www.landbigfish.com/staterecords/fishrecords.cfm? ID=112; accessed 13 January 2016)

State/Province	Weight (kg)	Weight (lbs)	TL (cm)	TL (in)	Location	Year
Michigan	87.5	193	221	87	Mullet Lake	1974
Minnesota	42.8	94	178	70	Kettle River	1994
Ontario	76.2	168	175	69	Nottawasga River, Georgian Bay	1982
Saskatchewan	122.5	270			South Saskatchewan River	1962
Wisconsin (spearing)	96.3	212	214	84	Lake Winnebago	2010

relationship as  $FL = (0.96223 \times TL) - 5.85734$  (Lowie et al., 2000). LS should be measured to the closest mm in total length (in lieu of fork length) in as consistent manner as possible to minimize measurement error and maximize precision.

### Age and size at maturity

The literature reports a wide range of sizes and ages of maturity for LS. Male LS have been reported to first mature at 76 cm (age 19-20) (Dubreuil and Cuerrier, 1950), 83 cm (age 14-15) (Probst, 1954; Cuerrier, 1966), 85-95 cm (ages 18-20) (Magnin, 1966), 102 cm (Bruch, 2008), and 114 cm (ages 14-16) (Priegel and Wirth, 1971). Female LS have been reported to first mature at 84 cm (age 26) (Dubreuil and Cuerrier, 1950), 90-100 cm (age 20-30) (Magnin, 1966), 122 cm (Bruch, 2008), 127 cm (age 22-25) (Probst, 1954; Cuerrier, 1966), and 139 cm (ages 24-26) (Priegel and Wirth, 1971). While variation in reported size at first maturity is not surprising for a slow growing, late maturing, and wide ranging fish like LS, it is likely that some of the spread in size and age at maturity could be attributed to factors such as limited sample sizes within a protracted size range of fish maturing for the first time and ageing error.

Male and female LS from the Winnebago System were found to reach maturity for the first time at 102 cm (age 14) and 122 cm (age 21) (Bruch, 2008), which are smaller sizes and younger ages than previously reported (Priegel and Wirth, 1975). Maturity modeling also revealed that the population of males in the Winnebago System requires 16 years (age 14–30) to become fully recruited to the adult stock, while females require 12 years (age 21–33) (Bruch, 2008). Female LS from the St. Lawrence River in Quebec were also found to exhibit a protracted age of first maturity with fish first recruited to the adult stock at age 15 with 100% recruitment at age 32, a span of 17 years (Fortin et al., 1992). The wide range of sizes and ages at first maturity may help explain, in addition to latitudinal differences in growth, the wide range of size and age of maturity of LS reported in the literature.

The sizes of first maturity of male and female LS from the Winnebago System were also estimated by Bruch (2008) as a function of  $L_{\infty}$  from invariate formulas (Froese and Binohlan, 2000) to be 94 cm for males, and 121 cm for females. These invariate driven estimates matched both of Bruch's (2008) maturity model estimates, 102 cm and 122 cm, and

empirical data from spawning assessments, 98 and 122 cm, quite well. In the models suggested by Froese and Binohlan (2000) asymptotic length explained 85% of the variation of length at first maturity in males and 91% in females (based on 467 pairs of  $L_m$  and  $L_\infty$  encompassing 265 species of fish from 3 classes, 27 orders, and 88 families including 2 species of sturgeon).

The protracted age of first maturity observed for LS of the Winnebago System and the St Lawrence River, Quebec, Canada (Fortin et al., 1992) suggests a life history trait common for the family. A protracted age of first maturity has also been suggested for Shortnose Sturgeon (Acipenser brevirostrum) (SNS) in the Saint John River estuary, New Brunswick, Canada (Dadswell, 1979), Kaluga (Huso dauricus) in the Amur River, Russia (Krykhtin, 1986), and Atlantic Sturgeon (Acipenser oxyrinchus oxyrinchus) (AS) in the Hudson River, New York, USA (Van Eenenaam et al., 1996) indicating this life history trait may be common to many of the species within the family Acipenseridae. Literature citations, when reporting size and age of maturity of sturgeon typically provide estimates of size and age of first maturity, but rarely provide the size and age of full recruitment of males and females to the mature stock. The long span of time from earliest to latest maturation of individuals in a sturgeon stock, and relatively old age of 50% maturity provides additional insight into the vulnerability of sturgeon stocks to recruitment overfishing and to why so many stocks have quickly collapsed when subjected to high harvest rates.

#### **Fecundity**

Fecundity of LS has been reported by Cuerrier (1949 – original data cited in Harkness and Dymond, 1961), Dubreuil and Cuerrier (1950), Harkness and Dymond (1961), Sandilands (1987), and Bruch et al. (2007; Table 5). All of these studies examined a relatively low number of fish, and, except for Bruch et al. (2007), it is unknown whether the authors accounted for ovarian tissue mass or volume, or whether the ovaries examined were in an F4 or 'black egg' stage of development (Bruch et al., 2001). Knowledge of fecundity is important not only for increasing the basic understanding of LS life history, but also to allow the use of fecundity as a variable in population dynamic modeling exercises. Bruch et al. (2007) suggested the following models for estimating LS fecundity for the Winnebago system:

Table 5
Lake sturgeon fecundity and related data reported in literature

Study	Origin	Number of fish examined	Mean fish weight (kg)	Estimated mean fecundity	Mean number of eggs per kg of fish
Cuerrier (1949)	Lake St. Peter, Ontario, Canada	9	23.9	295 573	12 264
Dubreuil and Cuerrier (1950)	Ottawa River, Canada	4	9.0	118 205	11 467
von Bayer (1910) and Harkness and Dymond (1961) <sup>1</sup>	Lake Erie	3	65.6	583 661	8744
Sandilands (1987)	Kenogami River, Ontario, Canada	2	13.3	120 998	8797
Bruch et al. (2007)	Lake Winnebago System, Wisconsin, USA	14	28.5	323 684	11 228

<sup>&</sup>lt;sup>1</sup>Harkness and Dymond used von Bayer's reporting of lake sturgeon egg diameter of 2.6 mm to volumetrically estimate the number of eggs in three Lake Erie fish whose roe was processed for caviar.

$$Ln(fec) = Ln(1661.936) + 1.566789(LnW)$$
  
or  
 $fec = 1661.946(W^{1.566789}),$ 

where fec is estimated fecundity; W is the fish weight; alpha = 1661.936; beta = 1.566789 ( $r^2$  of 0.66, F value = 23.2;  $P \le 0.001$ ).

# Population models

Developing functional and useful population models for any fish species requires data to be consistently collected over many years. This may be problematic for sturgeon given their long life span and difficulties encountered when attempting to sample populations. Models characterizing metrics such as age, growth, fecundity, weight-length, and eggs per recruit are fairly straightforward and not as data intense as models providing long term estimates of mortality and recruitment rates. All of these models (provided they are built with quality data) provide insights into the dynamics of a sturgeon population that are critical for effective management, especially if the population is exploited through recreational, commercial, and/or tribal fisheries.

Population models have been used successfully to better understand the population dynamics and set harvest limits for species such as Yellow Perch (*Perca flavescens*) (Wilberg et al., 2005), Lake Trout (*Salvelinus namaycush*) (Linton et al., 2007), and Lake Whitefish (*Coregonus clupeaformis*) (Ebener et al., 2005), but they have had little application as a tool to better understand or manage sturgeon populations or harvest. At issue of course is first having accurate age data (which is typically very problematic for sturgeon as most structures systematically underestimate the age of older fish) that spans a long enough time series. Pine et al. (2001) estimated a total annual mortality rate of 16% using an age-structured cohort analysis model to examine population growth and mortality trends of the Gulf Sturgeon (*Acipenser oxyrinchus desotoi*) (GS) over a

10-year period, 1986–95. Haxton et al. (2014a) used a Bayesian approach with a surplus production model to estimate LS abundance and intrinsic rate of increase for the Great Lakes prior to the high exploitation period beginning in the late 1800s. Few other references of agestructured analysis on sturgeon exist in the literature, likely due to the lack of long term catch at age data for sturgeon fisheries, in part because most sturgeon fisheries have been shut down.

Using 60 years of Winnebago LS harvest data, Bruch (2008) developed a statistical catch at age model (SCAA), as well as a series of other models, to estimate various LS population metrics and parameters including: intrinsic rate of population increase, natural mortality rate, length infinity, stock-recruitment parameters, and  $F_{0.1}$  yield per recruit. Haxton et al. (2014a) and T. J. Haxton (Ontario Ministry of Natural Resources (OMNR), Peterborough, ON, unpubl. data) also estimated some LS parameters including historic intrinsic rate of population increase for the Great Lakes, and LS growth model parameters and metrics for LS populations across Canada. These parameter estimates are listed in Table 6.

While simulation modeling can be used to predict a sturgeon population's sustainability and assess extinction risk from alternative management strategies, sufficient long term sturgeon population data are often not available to allow estimation of model parameters with confidence. Thirty years of sturgeon catch data from the lower Danube River in Serbia were used to predict the extinction of the Beluga (Huso huso) in 450 years, and Russian Sturgeon (Acipenser gueldenstaedtii) in 50 years (Lenhardt et al., 2006). Twentyfour years of demographic population assessment data were used to predict the extinction in 30 years of the endangered White Sturgeon (Acipenser transmontanus) (WS) in Kootenai River, Idaho, USA (Paragamian and Beamesderfer, 2004). A long term stochastic trends simulation model for the Winnebago System LS population utilizing 60 years of harvest and population assessment data and parameters from SCAA and stock-recruitment models found that the Winnebago LS population could be maintained at stable levels capable of supporting the annual winter spear fishery at exploitation rates up to the current limit of 4.7%. This was

Table 6 LS population dynamic parameter and metric estimates from Great Lakes region and Canada (r = intrinsic rate of population increase: M = natural mortality rate (age 1 and older);  $L_{\infty}$  = length infinity (cm) from von Bertalanffy (vB) model; K = Brody growth coefficient from vB model; YPR F<sub>0.1</sub> = yield per recruit at a fishing mortality rate 10% of maximum in kg/recruit and a recruit size of 95 cm and age of 12 years and an annual exploitation rate of 3.8%; u max = sustainable annual exploitation rate). (Haxton p.c. = pers. comm. Haxton, T., Ontario Ministry of Natural Resources, Peterborough, ON

Location, sample type (reference)	Sample type	r	M	$L_{\infty}$	K	YPR $F_{0.1}$	u max
Winnebago System unsexed (Bruch, 2008)	Unsexed	0.049-0.138	0.055			2.83	4.7%
Winnebago System (Bruch, 2008)	YOY			21.7	16.70		
Winnebago System (Bruch, 2008)	Juvenile age 1-12			98.1	0.230		
Winnebago System (Bruch, 2008)	Male age 13–69			166.4	0.052		
Winnebago System (Bruch, 2008)	Female age 13–96			188.9	0.045		
Great Lakes (Haxton et al., 2014a)	Unsexed	0.079 - 0.123					2.0-3.1%
Attawapiskat River (Haxton p.c.)	Unsexed			142.1	0.04		
Lake Huron (Haxton p.c.)	Unsexed			163.2	0.09		
Lake Nippissing	Unsexed			165.4	0.08		
Ottawa River (Haxton p.c.)	Unsexed			131.9	0.06		
Rainy River (Haxton p.c.)	Unsexed			166.5	0.06		
Winnipeg River (Haxton p.c.)	Unsexed			166.4	0.06		

corroborated with a surplus production model estimating sustainable exploitation rates of 4% (2.4–6.1%; Haxton et al., 2014a). Annual exploitation maintained at an average of 3.2%, the average rate from 1997 to 2007, would result in a robust stock of adult females, but at a level 28.3% less than the estimated abundance of the stock with 0% exploitation (Bruch, 2008).

While limited in number, the available sturgeon population simulation models support the common paradigm that sturgeon are very susceptible to overharvest and provides some insight into possible dynamics of stocks exploited at various levels. A modest increase in total annual mortality from 16% to 20% was predicted to cause the GS to decline towards extinction (Pine et al., 2001). Similarly, Shovelnose Sturgeon (Scaphirhynchus platorynchus) (SVS) in the Missouri River System were sensitive to even low levels of exploitation (Quist et al., 2002). The simulation model for LS of the Winnebago System predicted a decline in adult stocks to lower and lower levels as exploitation increased from zero. Despite being at lower levels the population appeared to be relatively stable until the number of adult females dropped below 300 and exploitation persisted at 20% or more, after which the model predicted the population was driven to extinction (Bruch, 2008).

#### Recruitment

Young sturgeon (in the first few years of life) are often difficult to capture in a consistent and reliable manner (Kempinger, 1996; Kennedy et al., 2007; Paragamian and Hansen, 2008), therefore recruitment estimates and stock recruitment models are lacking in the sturgeon literature. Recruitment estimates for sturgeon populations have typically been made through hindcasts of age estimates (Thomas and Haas, 2001; Quist et al., 2002; Woodland and Secor, 2007) or catch rates of first recruits to the fishery (Priegel and Wirth, 1975; Baker, 1980). Accurate recruitment estimates from hindcasts assume that age estimation error is low enough to accurately identify birth years, whereas pectoral fin rays systematically

underestimate the age of fish age 14 and older (Bruch et al., 2009). Furthermore, age estimates derived from pectoral fin rays sampled from known-age fish (ages 6–14) from the Winnebago System yielded poor precision between readers, suggesting that age data even on younger fish may not adequately track individual year classes [R. Koenigs, WI Department of Natural Resources (WDNR), Oshkosh, WI, unpubl. data]. While age estimates from other sturgeon species and populations may not exhibit the same error observed for LS from the Winnebago System, the likelihood of significant error is high and therefore needs to be considered when using ageing data to estimate recruitment. Estimating recruitment through catch rate of new recruits into a fishery may also be prone to error if ages assigned are inaccurate.

While the literature offers little quantitative information about LS recruitment, Bruch (2008) estimated the number of LS yearling recruits and 21-year-old female recruits in the Winnebago System from a SCAA model based on age data corrected for age estimation error for the years 1954–2007. The stock–recruitment relationship between adult females and yearling recruits was best defined by a Ricker model:

$$R_i = 20.07706 \times S \times e^{(-0.000445 \times S)} + \varepsilon$$

where model parameters  $\alpha = 20.07706$ , and  $\beta = 0.000445$ , and R = the number of yearling recruits produced by S, the number of adult females in the stock the year prior, and  $\varepsilon$  representing stochastic error.

The stock-recruitment relationship between adult females and 21-year-old female recruits was best defined by a Ricker model:

$$R_i = 2.99395 \times S \times e^{(-0.000436 \times S)} + \varepsilon,$$

where model parameters  $\alpha = 2.99395$ , and  $\beta = 0.000436$ , and R = the number of 21-year-old female recruits produced by S, the number of adult females in the stock 21 years prior, and  $\varepsilon$  representing stochastic error.

Further, Bruch (2008) reported that the yearling/adult estimate from SCAA models was 0.941 (SD 0.974) and that adult stock density heavily influenced yearling/adult estimates (range 0.011–2.597 yearlings per adult). The strength of the inverse S–R relationship was surprising given that LS in the Winnebago System were never observed preying on their young (Stelzer et al., 2008), although LS have been often observed preying on their eggs (Bruch and Binkowski, 2002). Paragamian and Hansen (2008) applied a stochastic density dependent simulation model to estimate that a recruitment level of 0.4 yearlings per adult was needed for recovery of the Kootenai River WS population in Idaho, USA.

If other sturgeon species or populations have recruitment rates as wide-ranging and exhibiting density dependent Ricker stock-recruit patterns similar to those suggested by the Winnebago System LS SCAA model, it, may be difficult to discern these relationships for stocks at low adult densities, or for populations with insufficient data to model recruitment. On the other hand, low density sturgeon populations with a Ricker style stock—recruit relationship should have good potential to produce large numbers of yearling recruits providing adequate spawning and nursery habitats are available and adult abundance has not dipped below a critical threshold. For example, the greatest yearlings/adult production for the Winnebago stock (2.590), was estimated from a point of lowest adult density (7302) in 1968 (Bruch, 2008).

### Mortality

Natural mortality is generally estimated by subtracting an estimate of instantaneous fishing mortality (F) from total instantaneous mortality (Z), which can be estimated as the negative slope of the descending arm of a catch curve (Ricker, 1975). However, catch curves are only as accurate as the age estimates that produced them. Given the potential sturgeon age error issues (Bruch et al., 2009), it is probable that the majority of catch curves previously developed for sturgeon using un-validated age estimates produced inaccurate over-estimates of Z. Instantaneous natural mortality rates (M) of LS populations have been estimated at 0.076 (Black Lake, MI, Baker, 1982), 0.072 (Groundhog and Mattagami Rivers, Ontario, Nowak and Jessop, 1987), 0.12-0.20 (St. Lawrence River, Quebec, Dumont et al., 1987), and 0.055 (Bruch, 2008). Bruch (2008) used corrected age data incorporated into a SCAA model to estimate instantaneous natural mortality (M) of 0.055, and a conditional natural mortality rates (n) for age 1 and older LS of 5.4%. Pauly's (1980) equation applied to the same Winnebago LS data estimated instantaneous and conditional natural mortality to be 0.0715 and 6.9% (Bruch, 2008). Pauley's equation (Pauly, 1980), has also been used to produce estimates of M of 0.049-0.70 for WS in the lower Columbia River, Oregon and Washington, USA (Beamesderfer et al., 1995), and 0.04 for Beluga in the southern Caspian Sea, Iran (Taghavi, 2001).

Estimates of M of other sturgeon species derived from catch curves include 0.020 for SNS in the Hudson River,

New York, USA (Woodland, 2005), 0.108–0.138 for SNS in the St. John River Estuary, New Brunswick, Canada, 0.07 for Pallid Sturgeon (*Scaphirhynchus albus*) (PS) in the Mississippi River, USA (Killgore et al., 2007), 0.10 for WS in the lower Columbia River, Oregon and Washington, USA (DeVore et al., 1995), and 0.092 for WS in the Kootenai River, British Columbia, Canada, and Montana and Idaho, USA (Paragamian et al., 2005).

Taghavi (2001) also used a model suggested by Richter and Efanov (1976) using age of 50% maturity to estimate M:

$$M = (1.521/t_{50\%\text{Mat}}^{0.72}) - 0.155,$$

where:  $t_{50\%\text{Mat}} = \text{age of } 50\%$  maturity, which provided estimates of M for male and female Beluga of 0.05 ( $t_{50\%}$  Mat = 16) and 0.03 ( $t_{50\%\text{Mat}} = 18$ ). Bruch (2008) applied the  $t_{50\%\text{Mat}}$  formula to male and female maturity data (19 and 27) from Winnebago System LS to derive estimates of M of 0.028 and -0.013 (a negative M for females).

Finally, Kennedy and Sutton (2007) used a model suggested by Hoenig (1983) relating total instantaneous mortality to fish maximum age:

$$LnZ = 1.46 - 1.01 \times Lnt_{max},$$

to estimate an M of 0.115 for SVS in the upper Wabash River, Indiana, USA. Applying this model to LS demographics from the Winnebago System, Bruch (2008) estimated M's of 0.035 for males and 0.001 for females (given empirical estimates of F and  $t_{\rm max}$  for males and females of 0.024, 70, and 0.040, 100).

While it is well understood that pectoral fin rays, and other aging structures underestimate that age of older fish (Bruch et al., 2009), underestimating the age of older fish leads to overestimates of Z and consequently M, if F is accurately estimated. Despite the potential error from use of unvalidated age data, and the potential shortcomings of generic mortality models, nearly all of the estimates of natural mortality for the various sturgeon species listed above are low and within a range that would be expected for slow-growing, late maturing, and long-lived animals exhibiting a k-selected or periodic (Winemiller and Rose, 1992) life history strategy.

Obviously the generic formulas for estimating M have important utility in the absence of other data for a particular fish stock, but their utility is somewhat limited, and until independent estimates of M are developed for various species and stocks, it is probably prudent to be careful about application of M estimates from these formulas, especially for species with intrinsically low M's. The SCAA model estimate of 0.055 for Winnebago LS (Bruch, 2008) was developed using unsexed catch at age data. Given the differences in life history and dimorphic growth patterns exhibited by males and females (Bruch, 2008), it is reasonable to suspect that male and female LS may experience different natural mortality rates. An additional attribute of M more difficult to evaluate is its variability. Catch curve analysis could potentially provide some insight into M's variability, but the error inherent in sturgeon age data may mask our ability to confidently determine the potentially narrow range of natural variation in M.

# Species habitat requirements, preferences and tolerances Habitat requirements and use

Lake Sturgeon are potamodromous and fluvial-dependent (Bemis and Kynard, 1997; Randall, 2008). However, they are known to tolerate brackish waters such as in the lower St. Lawrence River and in James and Hudson Bays (LeBreton and Beamish, 1998). Habitat requirements for LS vary seasonally and ontogenetically (Table 7). In rivers, LS spawning habitat is generally found in fast flowing areas of relatively shallow, well-oxygenated waters which are often below natural rapids, a dam, or an impassable barrier. Although LS are thought of as being philopatric, which has contributed to population structuring within large lakes (DeHaan et al., 2006; Welsh et al., 2008; Homola et al., 2010; Kerr, 2011), the species is also known for 'wandering' from home waters to take up residence and even join spawning groups in waters hundreds of kilometers away from home (R.M. Bruch, WDNR, Oshkosh, WI, unpbl. data; M. Donofrio, WDNR, Peshtigo, WI, pers. comm.; Heinrich and Friday, 2014). Spawning generally occurs in water depths 0.1-6.0 m (LaHaye et al., 1992; Lane et al., 1996; Threader et al., 1998; Bruch and Binkowski, 2002; Wilson and McKinley, 2004; Chiotti et al., 2008), however, LS may spawn in deeper (up

to 12 m) areas with adequate flows and substrate (Manny and Kennedy, 2002). Spawning flows are highly variable among populations but are generally between 0.34 and 2.0 m s<sup>-1</sup> (Threader et al., 1998; Billard and Lecointre, 2001; Caswell et al., 2004; Johnson et al., 2006; Peterson et al., 2007; Chiotti et al., 2008). Spawning does not appear to consistently occur in areas with flows exceeding 2 m s<sup>-1</sup> (LaHaye and Fortin, 1990) or  $<0.5 \text{ m s}^{-1}$  (R.M. Bruch, WDNR, Oshkosh, WI, unpbl. data). In lakes, LS have also been observed spawning on rocky wave-exposed shoreline or areas having strong wind and/or stream driven currents (Nevin, 1919; Galarowicz, 2003). Spawning areas are generally comprised of coarse (>2.1 mm) substrate (Peterson et al., 2007; Daugherty et al., 2008), with a preference to cobble and boulders (Threader et al., 1998) or coarse substrate interspersed with boulders and large rocks (LaHaye et al., 1992; Lane et al., 1996; Desloges et al., 2004). The availability of suitable spawning substrate is believed to be critical for reproductive success (Bemis and Kynard, 1997).

Habitat requirements of YOY and juvenile LS remains one of the largest information gaps pertaining to LS biology. LS YOY and juveniles generally select sandy areas devoid of vegetation (Kempinger, 1996; Peake, 1999; Benson et al.,

Life stage	Habitat characteristics	Preferred (range)
Spawning	Water depth (m)	0.5–3.0 (0.3–10.0) Staging areas 2.0–10.0 m deep
	Water velocity (m s <sup>-1</sup> )	0.5–2.0 (0.1–2.5)
	Substrate	Coarse cobble, rubble and boulders.
	Water temperature (°C)	12.0–16.0 (10.0–21.0)
Young-of-Year	Water depth (m)	Relatively shallow (2-5 m)
	Water velocity (m s <sup>-1</sup> )	Reduced ( $< 1-2$ cm s <sup>-1</sup> ) but detectable current
	Substrate	Fine substrates (sand and silt) devoid of vegetation
	Water temperature (°C)	14.0–17.0
Subadult	Water depth (m)	5.0-10.0 (2.0-60.0)
	Water velocity (cm s <sup>-1</sup> )	Detectable to moderate (25.0–50.0) current preferred (10.0–75.0)
	Substrate	Clean sand, gravel, or clay substrates
	Water temperature (°C)	< 20.0
Adult	Water depth (m)	Relatively shallow (3.0–5.0) areas Overwinter pools 6.0–11.0 in depth
	Water velocity (cm s <sup>-1</sup> )	< 70.0 (0.0–80.0)
	Substrate	Flat areas having silt, sand or clay substrate
	Water temperature (°C)	< 20.0

Table 7 General habitat requirements of lake sturgeon by life stage (from Kerr et al., 2011)

2005; Smith and King, 2005b; Kerr et al., 2011). Juvenile LS have also been observed in areas of sand and pea gravel immediately below woody debris (Holtgren and Auer, 2004) and organic substrate types (Smith and King, 2005b). Although YOY LS generally have been observed to select shallow areas <2 m (Benson et al., 2005), more specifically, 0.2–0.55 m deep (Ecologistics Limited, 1987; Friday, 2006) or <0.75 m deep (Kempinger, 1996), YOY have also been observed to utilize deeper offshore habitat at mean depths of 9 m (Smith and King, 2005b). YOY and juvenile LS are typically observed in water velocities <0.3 m s $^{-1}$  (Friday, 2006) to <0.6 m s $^{-1}$  (Benson et al., 2005).

Field studies indicate that LS appear to spend most of their first summer in the lower stretches of spawning rivers and adjacent bays (Auer and Baker, 2002; Baker, 2006; Daugherty et al., 2008), with some age-0 LS leaving their natal river as water temperatures decline (Caroffino et al., 2009) and as gravid adults move upriver to winter pre-spawn staging areas (R.M. Bruch, WDNR, Oshkosh, WI, unpubl. data,). Yearling LS are often found in bays or near a river mouth (Harkness and Dymond, 1961). Subadults [individuals >80 cm TL, <115 cm TL, and approximately age 15 (Haxton et al., 2008)] are believed to occupy different habitat types than adult LS. They are often found in deeper offshore waters of lakes (Smith and King, 2005b). Overall, early life stages of LS select habitats providing an abundance of food along with protection from predators (Randall, 2008).

Juvenile LS, the stage from YOY (i.e., yearlings) to the onset of maturity including subadults, demonstrate high site fidelity and display localized movement (Haxton, 2003; Lord, 2007). Juveniles (subadults) generally select deeper water depths than adults (Holtgren and Auer, 2004; Smith and King, 2005b) and are generally found in water depths 3-8 m (Harkness and Dymond, 1961; Threader et al., 1998; Nilo et al., 2006), but rarely in depths >14 m (Threader et al., 1998). Holtgren and Auer (2004), however, captured juveniles from depths 4-17 m, often in depths >10 m, whereas Smith and King (2005b) captured juvenile LS from depths of 5.4-13.4 m. In large, deep rivers, juveniles were selective to 12-18 m (Lord, 2007; Haxton, 2011), and purportedly seek deeper sections of rivers (Smith and King, 2005b; Barth et al., 2009). Habitat preference is perceived to be largely determined by food abundance (Chiasson et al., 1997; Beamish et al., 1998) however, food availability is not necessarily always the primary factor (Nilo et al., 2006). Sandy habitat is preferred (Mosindy and Rusak, 1991; Lane et al., 1996; Chiasson et al., 1997; Benson et al., 2005; McCabe et al., 2006; Nilo et al., 2006), but juveniles will also select gravel (Smith and King, 2005b; McCabe et al., 2006; Lord, 2007), clay (LaHaye, 1982; Chiasson et al., 1997), and organic substrates (Smith and King, 2005b; McCabe et al., 2006). Flow velocities of 0.4-0.75 m s<sup>-1</sup> (Threader et al., 1998) or 0.25-0.5 m s<sup>-1</sup> (Nilo, 1996) are preferred. Juveniles have rarely been found in velocities exceeding 0.7 m s<sup>-1</sup> (Billard and Lecointre, 2001).

Adult LS are bottom dwellers, prefer moderately turbid waters, and often frequent productive lake shoals and river deltas (Cech and Doroshov, 2004). They have been mostly observed residing in shallow water, preferring depths 3–9 m

(Houston, 1987; Knights et al., 2002; Smith, 2003; Wilson and McKinley, 2004), but have been caught as deeps as 43 m (Harkness and Dymond, 1961; Scott and Crossman, 1973). Habitat selectivity is highly variable among LS adult populations and is dependent on habitat available in the waterbody (Haxton et al., 2008). Silt, or mixture of silt/sand is preferred substrate (Haugen, 1969; Morse et al., 1997; Threader et al., 1998; Knights et al., 2002), however, LS have also been reported to select for organic (Hay-Chmielewski, 1987; Morse et al., 1997; Nilo et al., 2006), clay (Chiasson et al., 1997), sand, gravel and rubble substrates (Seyler, 1997). Adult LS are rarely found among aquatic vegetation (Baker, 2006).

Lake Sturgeon have been found to select and congregate in pools for overwintering (Harkness and Dymond, 1961; Kerr, 2011). These sites are generally 6–11 m in depth (McKinley et al., 1998; Threader et al., 1998) but rarely deeper than 10 m in Lake of the Woods (Rusak and Mosindy, 1997).

#### Food habits

Lake Sturgeon have historically been thought to be generalist opportunistic benthic feeders that preyed primarily on the most available and abundant benthic macroinvertebrates in the specific system the LS population happened to be residing in. Typical prey items historically reported included various species of Ephemeroptera, Diptera, Mollusca, and Decapoda with fish present as an occasional and almost accidental ingestion (Bajkov, 1930; Schneberger and Woodbury, 1946; Probst and Cooper, 1954; Harkness and Dymond, 1961; Magnin and Harper, 1970; Priegel and Wirth, 1971; Magnin, 1977). Diet studies on LS since the early 1990s have confirmed the importance of benthic macroinvertebrates in the LS diet throughout its range, but have also revealed that the species will consume large quantities of fish, plankton, and their own eggs in some situations and/or life history stages. Choudhury and Dick (1993) characterized the gastrointestinal parasite assemblage of LS in the Winnebago System, Wisconsin, They found no fish in the samples they examined at that time, but found significant seasonal variation in prey selection by adults residing in Lake Winnebago, including substantial quantities of Cladocera, primarily Daphnia and Leptodora spp., in summer samples. Stelzer et al. (2008) reported a significant shift in the diet of adult LS in the Winnebago System between the early 1990s and the mid 2000s from strictly invertebrates to a mix of invertebrates and fish. Using stable isotope analysis Stelzer et al. (2008) showed that by the mid-2000s LS in the Winnebago System were acquiring 37% of their carbon from fish, exclusively Gizzard Shad (Dorosoma cepedianum) during the winter months when the shad experience an annual die-off and litter the bottom of the lake making them easy prey for foraging LS. Smith et al. (2016) also found that LS in the Rainy River System, Ontario also obtain a large portion of their energy from fish in their diet. Bruch and Binkowski (2002) reported observing LS, especially males, ingesting LS eggs on LS spawning sites in the Wolf River, Wisconsin in between spawning bouts with ovulating females or after spawning was completed at a site.

The results reported by Choudhury and Dick (1993), Stelzer et al. (2008), and Smith et al. (2016) reinforce the early conclusion that LS are indeed opportunistic feeders that will also feed pelagically for plankton and eat large quantities of fish if they are readily available. Recent work has shown that LS will also adapt quite readily to new prey items that come upon the scene. Gizzard Shad were rare in the Winnebago System prior to the early 1990s but became quite common and very abundant in the System in some years by the mid to late 1990s (R. Koenigs, WI DNR, Oshkosh, WI, pers. comm.). After zebra mussels (Dreissena polymorpha) became established and abundant in Oneida Lake, New York, LS began to utilize them as prey becoming the dominant prey item in fish >900 mm (de Lafontaine and Costan, 2002). Interesting though is the insignificant amount and occurrence of zebra mussels found in the diet of LS in the Winnebago System after the mussels became established and extremely abundant in those waters (Stelzer et al., 2008; R. Koenigs, WDNR, Oshkosh, WI, pers. comm.). These findings reaffirm other recent observations by Nilo et al. (2006) and Smith et al. (2016) that the species, while opportunistic, will be somewhat selective when choosing their prey, especially seasonally.

In summary, LS can be categorized as generalist opportunistic feeders, that also exhibit some seasonal prey selectivity as well as planktonic and pisciverous feeding behavior, including active feeding on their own eggs laid at spawning sites.

### Ontogenetic migrations

LS are potamodromous, migrating strictly within freshwater (Scholl, 1986; Kempinger, 1988; Rusak and Mosindy, 1997; Auer, 1999a,b; Knights et al., 2002). Due to their extensive migrations to feed and spawn, LS require watersheds having diverse and unobstructed habitat (Beamesderfer and Farr, 1997; Earle, 2002). Although Auer (1996a) suggested that a barrier-free distance of at least 250–300 km of lake/river range should be maintained to support self-sustaining LS populations, numerous populations in fragmented river systems maintain viable populations in sections of river as short as 45 km (Scholl, 1986; WDNR, 2000; Barth et al., 2011).

Changes in water temperature, water level and flows all provide environmental cues to LS (Auer and Baker, 2002; Bruch and Binkowski, 2002; Wishingrad et al., 2014). Natural flow regimes are important and sudden changes in river flow can initiate movements. Generally, LS have the tendency to move upstream during periods of increased discharge and drop back downstream when flows are decreasing (Borkholder et al., 2002). Similar seasonal movements are noted in spring and autumn (Kampa et al., 2014).

Lake Sturgeon will migrate upstream past seemingly ideal spawning areas to spawn at sites further upstream (Harkness and Dymond, 1961; Bruch and Binkowski, 2002), and will consistently spawn at the base of dams (Kempinger, 1988; LaHaye et al., 1992; Auer, 1996a,b, 1999b; D'Amours et al., 2001; Bruch and Binkowski, 2002; Haxton, 2003). Prolonged swimming speeds have been found to be 45–75 cm s<sup>-1</sup> with burst speeds in the range of 75–85 cm s<sup>-1</sup> (Hoover et al.,

2005). Migrations to spawning areas can occur either in the autumn or the spring (Bemis and Kynard, 1997). Staging areas in close proximity (<3 km) to spawning sites are important regardless of the timing of pre-spawn migrations (Daugherty et al., 2008).

Lake Sturgeon seemingly possess homing tendencies which enables them to return to their natal river or watershed (Boiko, 1993; Bemis and Kynard, 1997; Bruch and Binkowski, 2002; Baker, 2006; DeHaan et al., 2006; Welsh et al., 2008). However, spawning site fidelity of LS may be relatively weak on systems with numerous spawning sites (R.M. Bruch, Koenigs, K., WDNR, Oshkosh, WI, unpubl. data). LS from the Winnebago System have been observed utilizing different sites, as well as different rivers, from one spawning year to the next Furthermore, males spawned at two or more sites in up to two different rivers within the same year (R.M. Bruch, Koenigs, K., WDNR, Oshkosh, WI, unpubl. data). The spawning migration behavior and site utilization of adults observed in the Winnebago System suggest that other LS populations exhibiting strong site fidelity may be doing so because suitable spawning habitat is limited on a consistent basis from year to year. Following spawning, adults generally return to feeding areas (Bemis and Kynard, 1997; Rusak and Mosindy, 1997; Thuemler, 1997; Bruch and Binkowski, 2002; Adams et al., 2006).

Following egg deposition at the spawning site, extensive egg predation may occur by LS, especially males, and other fish such as Catostomidae and Cyprinidae species, as well as by crayfish (Bruch and Binkowski, 2002). Paradoxically, the movement and feeding by predators actually cleans the substrate, which likely provides greater opportunity for water flow and circulation through the interstitial spaces where eggs are incubating below the substrate surface (Bruch and Binkowski, 2002). Mortality rates from eggs to YOY, and from larva to YOY on the Peshtigo River in Wisconsin, were estimated to be 99.9%, and 90.5–98.3% respectively (Caroffino et al., 2010).

Yolk-sac larvae emerge about 11–19 da post peak spawn (LaHaye et al., 1992; Smith, 2003; Smith and King, 2005a). Peak drift occurs nocturnally between 2100 and 0200 hours (Kempinger, 1988; D'Amours et al., 2001; Smith, 2003) and generally drift downstream with currents dispersing as it dissipates. Duration of drift varies but has the potential of extending up to 40 da (Auer and Baker, 2002) which may be up to 40–50 km from their natal site within the first month (Dick et al., 2006).

Outside of spawning migrations, LS can sometimes be rather sedentary (Fortin et al., 1993; Haxton, 2003; Barth et al., 2011). Most LS move within their home range of 12–14 km (Peterson et al., 2007; Kampa et al., 2014) and display site fidelity despite the potential to move extensively (Borkholder et al., 2002; Knights et al., 2002; Haxton, 2003; Barth et al., 2011; Gerig et al., 2011; McDougall et al., 2013), although extensive movement has been observed to occur (Knights et al., 2002; Shaw et al., 2013; Wishingrad et al., 2014). Differences in minimum distance moved is typically not detectable among sexes or among seasons, however putatively reproductively 'ready' females travelled greater distances than non-reproductive females (Shaw et al., 2013).

Juvenile movement can be quite restricted within a regulated river with the majority of fish remaining within 1.5 km of their capture site (Barth et al., 2011). In Portage Lake, Michigan, Holtgren and Auer (2004) found that diurnal movements of juvenile and subadult LS were related to light intensity, moving into shallow water at night and back to deep water during the day. Age-0 LS have also been observed being more active at night (Benson et al., 2005). Adult movement is generally greater than subadult and juveniles (Trested et al., 2011; McDougall et al., 2013) and it appears that the latter life stages may be limited by flows and natural constrictions within some rivers (McDougall et al., 2013).

Juvenile (Altenritter et al., 2013) and adult LS (McKinley et al., 1998; Threader et al., 1998; Wishingrad et al., 2014) often move to deep pools or a lake environment supporting relatively low water velocities during winters. There is evidence of fidelity to overwinter habitats (Auer, 1996a,b; Knights et al., 2002; Wishingrad et al., 2014) but not consistently (Rusak and Mosindy, 1997). During this time, they have often been found in aggregations and to display sedentary behaviour (Rusak and Mosindy, 1997; Kerr et al., 2011; Shaw et al., 2013). It has not been demonstrated how important these overwintering areas are for LS survival, but winter habitat selection may be a behavioural response to highly dynamic lotic systems.

# Reproduction and spawning

# Spawning behavior

Lake Sturgeon spawn in late spring/early summer, depending on location, at temperatures between 9 and 18°C (Harkness, 1923; Scott and Crossman, 1973; Bruch and Binkowski, 2002; Nicols et al., 2003; Heinrich and Friday, 2014), and often exhibit a protracted period in which two or more spawning peaks occur in the same season. Typically, the same males participate in all of the peaks even if they are spread out over a month or longer (Auer and Baker, 2002; Bruch and Binkowski, 2002; Nicols et al., 2003). Bruch and Binkowski (2002) made extensive field observations of spawning LS in the Wolf and upper Fox Rivers in Wisconsin over a 20-year period and succinctly summarized LS spawning behavior:

Lake sturgeon display an intricate set of sexual behavior responses to water temperature during their spawning period. When water temperatures rise to 6.6–16.0°C, sturgeon begin exhibiting a porpoising behavior in the vicinity of the spawning grounds. As the water continues to warm, this behavior increases in intensity and continues until slightly past the peak of spawning activity. In the range of 8.8–16.0°C, males move onto the spawning grounds and begin cruising, apparently searching for signs of ovulating females. Individual females will move onto a site at water temperatures of 8.8–19.1°C, with the maximum number of females and heaviest spawning activity on a site occurring generally within 11.5–16.0°C. Lake sturgeon were observed spawning both during the day and night at wide temperature ranges, 8.8–21.1°C.

Whereas males arrive first at the spawning site, females ultimately determine the duration of spawning through the timing and intensity of their use of that site. During the spawning act, activity also keys off the females, with the males responding to cues from the female to participate in 2-4 s spawning bouts during which a relatively small number of eggs (estimated 947-1444 eggs per bout) are released by the female into a cloud of sperm (estimated 200-800 billion sperm) from two to eight males. The males beat the abdomen of the female with their tails and caudal peduncles while ejaculating. While ejaculating, males emit a dull, thunderous vibrating sound which attracts other males to the area. The female initiates a spawning bout at approximately 1.5 min intervals and will continue oviposition for 8-12 h, even if the water temperature decreases or increases outside the optimal range (11.5-16.0°C). Spawning typically occurs for 2-4 days on each site, depending on the number of females utilizing the site. At cessation of the spawning season, Wolf River sturgeon quickly move back into the main river channel. While water temperature is a key environmental signal affecting the onset and duration of the spawning period, the rate of water temperature increase prior to spawning appears to influence the actual temperature at which spawning begins. Sturgeon exhibit complex polygamous mating behavior whereby several males may fertilize the eggs of a single female, and each male may participate in spawning with several females while on the spawning grounds. The breeding system is both polyandrous and polygynous, thereby maximizing the opportunities for mating with numerous individuals and subsequently maximizing the genetic diversity of the offspring.

Bruch and Binkowski (2002) also reported observing a phenomenon with LS spawning behavior in the Winnebago System known as the '2nd' and '3rd spawning runs', which has also been observed in other LS populations (Online at: http://www.sturgeonfortomorrow.org/research-2003-sum.php, accessed 1 May 2016; [P. Talmadge, MN Dept. of Natural Resources (MDNR), Baudette, MN, pers. comm.]. Based on over 20 years of observations and water temperature data before and during the LS spawning seasons on the Winnebago System LS were observed to sustain a second and sometimes a third separate subsequent period of spawning activity in the Wolf and Upper Fox Rivers in some but not every year. The phenomenon was typically observed in years when spring water temperatures slowly rose to a point to induce initial LS spawning activity, but then quickly dropped due to a cold front and/or snowfall. Initial spawning activity would continue until females that had begun ovulating and spawning were finished, but activity would not sustain as females that had not initiated spawning prior to the temperature drop would hold-off and wait until the water temperature would rise again with the next warm weather system. In these situations, the water temperatures needed to re-induce spawning activity were typically at a point that was higher than the temperatures were when initial spawning ended. Also, based on assessments made of LS captured during the

'1st', '2nd' and '3rd' runs on the Wolf River, the 1st run typically was always found to be the most robust with the largest number of females spawning, while the 2nd and, when occurring, 3rd runs were found to be comprised a small number of females that apparently spawned at higher temperatures, and large numbers of males that had remained in the river waiting to spawn with the females that had yet to ovulate. The period of time between 1st and 2nd runs was observed to be as much as 3-4 weeks in some years on the Wolf River, with males observed and captured during spawning in the 1st run, also observed spawning and captured during the 2nd and even 3rd runs, even if the subsequent spawning periods occurred weeks after the 1st (Bruch and Binkowski, 2002; R. Koenigs and R. Bruch, WDNR, Oshkosh, WI, unpubl. data; D. Folz, WDNR, Oshkosh, WI, pers. comm.).

#### Sound production during spawning

Lake Sturgeon have been found to make sounds associated with spawning. Bocast et al. (2014) recorded low fundamental frequency (5-8 Hz) drumming, rumble, and hydrodynamic sounds of male and female LS on the Wolf and Embarrass River Systems in Wisconsin during observed active LS spawning. Male LS were recorded making a distinctive drumming sound while ejaculating around the ovulating female during egg expulsion, also observed by Bruch and Binkowski (2002), which could break the surface of the water occasionally and propagate harmonics in the terrestrial atmosphere, creating the drumming sound known by local Native Americans as 'sturgeon thunder'. Bocast et al., 2014 further reported that females appeared to make a low frequency rumble or growling sound just prior to egg expulsion. All of the sounds recorded by Bocast et al. (2014) coalesce into a distinctive acoustic signature of lake sturgeon spawning activity. Knowledge of this signature and the equipment needed to capture the sounds could be used to document LS spawning activity which would be especially useful in systems where spawning can not be observed due to water depth and/or turbidity, or on systems where documentation of first spawning of restored populations is desired.

# External biology/functional morphology

Peterson et al. (2007) published a very comprehensive summary of external morphology of LS which has been reproduced as part of this paper:

The physical appearance of lake sturgeon [Fig. 3]) is similar to that of most other Acipenser species; and like all other members of the genus, they are easily recognized by

several primitive morphological features that distinguish them from other North American fishes. Perhaps the most noticeable of these is the scaleless body, which is protected by five lateral rows of bony plates or scutes. The heavy-set body is spindle shaped, the greatest body depth occurring slightly anterior to the midsection. The origin of the anal fin is located posterior to that of the dorsal, its tip rarely extending beyond the caudal fulcrate plate. Other morphological features that distinguish lake sturgeon from other North American freshwater fishes include a heavily armoured skull, a spiral valve intestine, and a cellular swim bladder that retains some of the lung-like characteristics of early actinopterigeans (Harkness and Dymond, 1961).

Basic morphology of the lake sturgeon is similar to that of other Acipenserids. The elongated body in cross-section is pentagonal in young juvenile specimens but becomes progressively more rounded with age (Scott and Crossman, 1973). Dorsal, lateral, and ventral scute counts are typically 9-17, 29-42, and 7-12, respectively. Dorsal fin rays number 35-45; anal fin rays 25-30 (Vladykov and Greeley, 1963; Scott and Crossman, 1973). The slightly upturned rostrum is disproportionately large in juveniles, often exceeding post-orbital distance in juveniles <50 cm; however, this proportion is gradually reversed with age (Vladykov and Greeley, 1963). The large, transverse mouth typically measures approximately 66-93% of the interorbital width (Vladykov and Greeley, 1963). The top lip is continuous; the bottom lip interrupted [Fig. 4]. Mouth shape and size in proportion to head width is most similar to that of shortnose sturgeon (A. breviostrum) (Vladykov and Greeley, 1963; Hochleitner and Vecsei, 2004). As in the elasmobranches, the sturgeon jaw is detached from the skull, allowing the mouth to project downward during feeding (Vecsei and Peterson, 2004). Lake sturgeon barbels are situated closer to the tip of the snout than to the origin of the mouth—an important diagnostic character distinguishing the species from acipenserids. Gill rakers are short and typically number 25-40 (Vladykov and Greeley, 1963). The thick-walled, gizzard-like stomach is connected to a spiral-valve intestine, a primitive alimentary arrangement shared by many Acipenserids adapted to a diet of benthic crustaceans and molluscs (Harkness and Dymond, 1961).

Body armouring is extensive on juveniles but becomes progressively reduced with age (Priegel and Wirth, 1971; Scott and Crossman, 1973; Vecsei and Peterson, 2004). In juveniles <100 cm, the laterodorsal and lateroventral

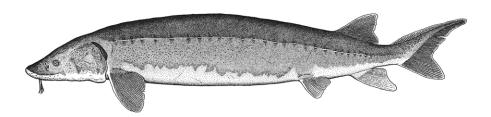


Fig. 3. Basic morphology of the adult LS (re-printed with permission from Springer and Peterson et al., 2007)

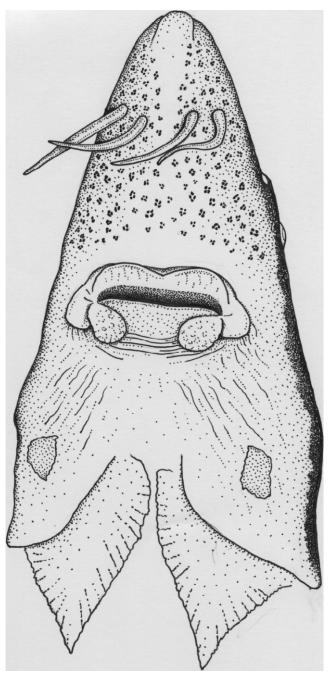


Fig. 4. Ventral view of LS head, showing distribution of sensory pits and relative position of barbels and mouth (re-printed with permission from Springer and Peterson et al., 2007)

surfaces are protected by a layer of tightly-spaced denticles evenly distributed between the five principal rows of scutes. Sharp, apical hooks are particularly prominent on the scutes of juveniles, but these gradually disappear with age until the scutes themselves are almost completely resorbed later in adulthood. In contrast, most anadromous sturgeons retain ossified scutes that continue to grow throughout their entire lifecycle. Hence, the process of scute resorbtion in adult lake sturgeon

probably illustrates an important trade-off in the functional morphology of body armouring within the genus. In freshwater environments devoid of sharks and other large biting predators, the protective advantage of body amour diminishes with increasing body size, yet the energetic costs of overcoming frictional drag caused by the rough armoured surfaces increases exponentially. By adulthood, lake sturgeon have simply outgrown all potential aquatic predators and hence, their need for body armouring.

The skull of all acipenserids, including the LS, is heavily armoured by a series of contiguous bony plates that are most apparent in juveniles and sub-adults [Fig. 5]. Variation and complexity in the ossification of the *Acipenser* skull roof has been noted by several researchers (e.g. Jollie, 1980); however, only the skull structure of shortnose sturgeon has been well studied (Hilton and Bemis, 1999). Although the LS skull is comparatively less variable, Jollie (1980) noted considerable intraspecific and ontogenetic variation.

Peterson et al. (2007) go on to say:

"In lake sturgeon the postdorsal plates are typically seen as 1–2 unpaired elements (Vladykov and Greeley, 1963; Peterson et al., 2003); however, the second predorsal may appear as a paired element in some individuals. The relatively large preanal plates always occur in single file and number 1–2 (Vecsei and Peterson, 2004). These ossifications may be considered definitive in all cases except on very old individuals where they may be completely resorbed.

Body coloration of lake sturgeon is variable among stocks but is typically dark brown or dark gray dorsally with a similar but slightly lighter coloration on the lateral surfaces. The ventrum is typically white or cream-colored. Some individuals have gray or black pigmentation on the underside of the head, particularly on the lips and barbels (Harkness and Dymond, 1961). Rarely, adults may exhibit white or milky blotches or spots on the lateral body surfaces. The dorsal and lateral scutes are typically the same color as the surrounding skin, although rare specimens may have slightly lighter lateral scutes or dark pigmentation on the lateral surfaces of the ventral scutes.

Although lake sturgeon exhibit considerable morphological ontogeny, the changes in color pattern from early juvenile to adulthood are among the most pronounced (Vladykov and Greeley, 1963; Priegel and Wirth, 1971; Peterson et al., 2003). In juveniles <30 cm, two large black saddles typically are present across the gray or brown dorsum and sides [Fig. 6]. Black speckling on the upper surfaces of the body also is common, often producing a 'peppered' appearance on the juveniles. Scutes and other dermal ossifications of juveniles are usually of the same color as the surrounding skin, but lateral scutes may sometimes be lighter (as in the adults). In 2–4 year-old

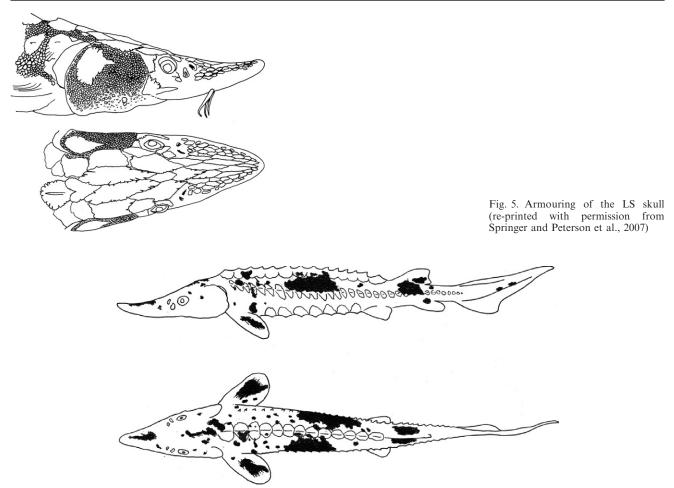


Fig. 6. Basic morphology and coloration of juvenile LS (<30 cm) (re-printed with permission from Springer and Peterson et al., 2007)

juveniles (>60 cm) the large saddle marks are lacking but the black speckling may persist into early adulthood."

## Internal biology

Sturgeon are unique, described as living fossils dating back to the Lower Jurassic some 200 million years ago (Bemis and Kynard, 1997; Bemis et al., 1997; Pikitch et al., 2005) that have changed very little morphologically (Choudhury and Dick, 1998a). The digestive system within North American sturgeon are very similar (Buddington and Christofferson, 1985), however, as a group they have unique features internally. LS possess a large, cellular swim bladder that retains some of the lung-like characteristics of early actinopterigeans (Harkness and Dymond, 1961; Singer et al., 1990 Peterson et al., 2007). The inside layer of the swimbladder contains isinglass, a gelatinous material that historically was sought for use in glue (Prince, 1905), used as a clarifying agent for beer and wines, and used in the preparation of jellies (Holzkamm and McCarthy, 1988).

The alimentary channel consists of the esophagus, stomach, pyloric stomach, upper intestine and spiral valve intestine (Kempinger, 1996) The pyloric stomach is a thick walled,

gizzard like stomach (i.e., pyloric caecum) used to grind prey (Nilo et al., 2006; Peterson et al., 2007) and is connected to the spiral valve which is considered a primitive arrangement (Harkness and Dymond, 1961; Peterson et al., 2007).

Male and female gonads in reproductively ready LS represent a significant portion of the peritoneum. Gametes are released into the peritoneal cavity, collected by the Meullerian ducts and transported to the urogenital pore.

Lake Sturgeon blood serum displays similar osmotic and ionic composition to other North American freshwater sturgeon species. Juvenile LS do not appear capable of homeostasis above 15‰ nor are they tolerant to environments exceeding 25‰. However, greater tolerance to elevated salinities was noted with increased size (LeBreton and Beamish, 1998). Lake Sturgeon use nonesterified fatty acids (NEFAs) for the mobilization of plasma lipids for energy metabolism and selectively mobilize different NEFAs depending on the season (McKinley et al., 1993).

### Parasites and diseases

Lake Sturgeon have been examined for disease and parasites extensively in Wisconsin, as the annual spear harvest on the Winnebago System provides the opportunity to collect the tissue samples needed for disease testing and parasite necropsies (WDNR, unpubl. data). Additionally, samples have been collected in Manitoba through cooperation with First Nation domestic and commercial sturgeon fishermen (Choudhury and Dick. 1993).

Lake Sturgeon harvested from the Winnebago System have been tested for WS Irido-like virus (WSIV), Largemouth Bass Virus (LMBV), Infectious Hematopoietic Necrosis (IHNV), Infectious Pancreatic Necrosis (IPNV), Viral Hemorrhagic Septicemia (VHSV), Oncorhynchus Masou Virus (OMV), Channel Catfish Virus (CCV), Renibacterium salmoninarum (Rsal), Yersinia ruckeri (Yruc), Aeromonas salmonicida (Asal), Myxobolus cerebralis (Mcer), and Bothriocephalus acheilognathi (Bach). Through 2012 sampling, all results have been negative except for positive hits of Rsal bacterium initially in 2002, and Yruc bacterium initially in 2011 (R. Koenigs, WDNR, Oshkosh, WI, unpubl. data.)

Lake Sturgeon have been challenged with VHSV in laboratory experiments conducted at Michigan State University to determine if the species was susceptible to and/or a carrier of the virus. Dr. Mohamed Faisal, DVM & Professor Aquatic Animal Medicine at Michigan State University reported study results on LS from his lab in a letter dated 28 September 2010 to Gary Whelan, Fish Production Manager of the Michigan Department of Natural Resources: "Lake sturgeon was found to be totally refractory to VHSV-IVb to the extent that when the virus was injected, it could not be reisolated or even detected by nested RT-PCR or quantitative PCR. The reason for this resistance to the virus deserves further investigation and is probably due to the lack of a receptor compatible with VHSV glycoproteins." As a result, LS are not listed as a VHS susceptible fish species.

Dr. Anindo Choudhury, St. Norbert College, DePere, WI, has extensively examined LS for parasites in both US and Canada. To date he has documented more than 20 different parasites in surveys of LS (Choudhury and Dick, 1993, 1998b; Choudhury et al., 1996), including descriptions of new species of nematode (Spinitectus acipernseri) gill fluke (Diclybothrium atriatum), and lastly an intestinal trematode fluke (family Deropristiidae) which he discovered in an individual LS from the Wolf River and named Pristicola bruchi (Choudhury and Dick, 1992; Choudhury, 2009). In addition, lake sturgeon is also a common host for the enigmatic cnidarian Polypodium hydriforme, a parasite that develops in the eggs of sturgeon and paddlefish; the parasite has been reported from Canada and the US (Choudhury and Dick, 1991; Raikova, 1994). The presence or absence of parasite species in individual LS was also found to be a strong indicator of diet and potentially home range locations for different life stages of individual fish (Choudhury et al., 1996). None of the diseases or parasites found in the testing referred to above were considered to be significant health threats to the LS populations that were sampled (Choudhury and Dick, 1993). Lake Sturgeon and their parasites have arguably been associated with each another for millions of years (Choudhury and Dick, 2001). More recently, researchers at Purdue University have found evidence of lateral transfer of some genes from an unknown schistosome-type trematode into the genome of LS, as well as molecular evidence of a protistan

parasite in the gonads (Hale et al., 2010). In contrast to most of the helminth parasites, the ectoparasitic Sea-Lamprey is a potential threat to LS populations in the Great Lakes; in experimental exposures, Sea Lamprey attacks resulted in decreased body condition and mortality, and these effects were especially lethal in younger sturgeon (Patrick et al., 2009). However, the implication of these findings for natural LS populations remains uncertain (Patrick et al., 2009).

#### Genetics

#### Chromosome number and ploidy

Lake Sturgeon have an estimated 240–268 chromosomes (Blacklidge and Bidwell, 1993; Fontana et al., 2004) with approximately 8.9 pg of DNA per cell (Blacklidge and Bidwell, 1993). Efforts to identify sex chromosomes in LS have been unsuccessful, possibly due to the complexity of the genome or that LS may not have sex chromosomes. Rather, sex may be determined by autosomal chromosomes or the environment (McCormick et al., 2008).

Much debate has surrounded the determination of ploidy level in LS. Initially, LS were thought to be octoploid through karyotype analysis (Blacklidge and Bidwell, 1993). However, subsequent karyotype characterization determined that LS were most likely tetraploid (Fontana et al., 2004), which has been further confirmed by the number of alleles observed at microsatellite loci (Ludwig et al., 2001) and inheritance studies using microsatellites (Pyatskowit et al., 2001; McQuown et al., 2002; Welsh and May, 2006). Microsatellite studies have demonstrated that the LS genome appears to be a mixture of tetrasomic and disomic loci, with 79% of the loci as tetrasomic and 21% of the loci as disomic (Welsh et al., 2003). Triploidy also appears to be relatively common in LS, indicating that the mechanisms of polyploidization may be a current evolutionary force acting on the LS genome (Blacklidge and Bidwell, 1993; Welsh and May, 2006). It has been hypothesized that the LS genome is evolving to the diploid state through a functional reduction in ploidy level (Ludwig et al., 2001). The extra chromosomal copies may not be functional variants, but may instead represent non-functional pseudogenes. The maintenance of multiple variants may reflect a slow rate of concerted evolution throughout the LS genome, reducing the rate of homogenization among chromosomal copies (Krieger and Fuerst, 2004).

# Genetic relationships to other sturgeon species

Mitochondrial DNA (mtDNA) has been used to identify phylogenetic relationships among sturgeon species. LS were identified as a sister group to the SNS (Krieger et al., 2000; Ludwig et al., 2001), confirming previous genetic studies documenting that relationship (Artyukhin, 1995; Brown et al., 1996). On a broader scale, LS are part of the Atlantic clade, which includes SNS and several European species (Ludwig et al., 2001). LS are not known to naturally hybridize with any other sturgeon species.

#### Population genetics

Genetic variation throughout the LS range has been assessed. Initially, it was thought that LS had low genetic variation. Early studies using mtDNA found only two haplotypes, with the majority of the sturgeon in the Great Lakes/St. Lawrence River having a single haplotype and LS in the Hudson Bay system having both haplotypes (Ferguson and Duckworth, 1997). Subsequent studies using a larger, more variable portion of the mtDNA have revealed significant mtDNA variation, with 22 haplotypes being identified in 11 populations in the Great Lakes (DeHaan et al., 2006).

The subsequent use of microsatellites has facilitated finer-scale delineation of LS population structure. The deepest level of genetic divergence is observed between LS in the Hudson Bay and Great Lakes systems (Welsh et al., 2008; McDermid et al., 2011). It has been hypothesized that this divergence may be due post-glacial colonization from different glacial refugia, with populations from northwestern Ontario and Lake Superior possibly having ancestry from the Missourian refugium and populations from the St. Lawrence River system originating from the Mississippian refugium (McDermid et al., 2011).

Within the Great Lakes basin, most populations have significant genetic differences, indicating the likelihood of natal fidelity (McQuown et al., 2003; DeHaan et al., 2006; Welsh et al., 2008). The highest levels of genetic differentiation within the Great Lakes were observed in Lake Superior and may be a result of natural migration barriers due to the geography of the lake (Welsh et al., 2008). There is genetic evidence for potential natural recolonization in the Great Lakes. Lake Sturgeon in the St. Clair River are genetically indistinguishable from LS in the Lower Niagara River, suggesting the possibility of population reestablishment at a location where sturgeon were thought to be extirpated (Welsh et al., 2008). Despite many populations in the Great Lakes having substantially reduced population sizes, remnant populations have appeared to retain relatively high levels of genetic diversity. No correlation between genetic diversity and population size has been observed (DeHaan et al., 2006).

Within the Hudson Bay system, population differences have been observed between river systems (McDermid et al., 2011). However, unlike the Great Lakes drainage, LS in the Hudson Bay system are primarily river residents, with multiple spawning groups existing in a single waterway. Genetic differences were not observed among spawning groups in connected waterbodies (e.g., southern and main stems of the Saskatchewan River; McDermid et al., 2011), despite the presence of potential natural barriers to upstream movement within a river system (Welsh and McLeod, 2010). Populations in the Hudson Bay system generally have lower genetic diversity relative to populations in the Great Lakes (Welsh et al., 2008; McDermid et al., 2011). However, as in the Great Lakes, levels of genetic diversity are not correlated to population abundance (McDermid et al., 2011).

Few natural populations of LS remain in the Mississippi River system. Those that do are genetically distinct from both the Great Lakes and Hudson Bay systems (Drauch et al., 2008). The White River population in Indiana is the last LS population in the Ohio River drainage. It has slightly lower genetic diversity than other LS populations, but the population does retain some unique genetic variants, indicating its potentially distinct evolutionary trajectory relative to other LS populations (Drauch et al., 2008). In the northern part of the Mississippi River system, the LS population in the east fork of the Chippewa River is more genetically similar to LS populations in the Great Lakes than to the White River population in the Ohio River (Drauch et al., 2008). However, although genetically distinct, the east fork of the Chippewa River in the northern portion of the Mississippi River is more closely related to Great Lakes populations than the population remaining in the Ohio River basin, with a low 3.5% straying rate (Homola et al., 2010). In Lake Michigan, high rates of straying were observed (average = 10%); these rates were asymmetrical and had high variance across populations (Homola et al., 2012). Despite these high rates of straying, significant genetic differentiation was observed among spawning populations, indicating these movements do not always result in successful reproduction (Homola et al., 2012). Assignment of individuals to their most likely spawning population has also provided data on which populations are being impacted by harvest (e.g., Bott et al., 2009) and which populations are colonizing restored habitat (Marranca et al., 2015).

As new genomic approaches become more accessible for non-model organisms like LS, genetic markers from throughout the genome will provide greater resolution for detecting population differences and for identifying adaptive variation. Lake Sturgeon can exhibit high individual repeatability regarding spawning time (i.e., early and late spawners) and breeding area within a spawning site (Forsythe et al., 2012). Therefore, genetic differences likely exist among these groups, but the current suite of microsatellite loci do not have sufficient power to detect these differences.

# Fisheries and impacts

There are 19 US states and Canadian provinces that recognize LS as a native species (Fig. 1). Two currently have commercial harvest fisheries, eight have recreational fisheries (four of which allow harvest while the others are catch and release only), and six have Tribal or First Nation fisheries and harvests (Table 8). The largest and most well-known LS fisheries are the commercial fishery in the St. Lawrence River in Quebec (annual harvest of about 80 000 kg) (Mailhot et al., 2011); the winter spear fishery on the Winnebago System in Wisconsin (annual harvest of 45 000 kg (~1000 LS) during the 2014 and 2015 seasons; (R. Koenigs, WDNR, Oshkosh, WI, unpubl. data) and the recreational hook and line fishery on Lake of the Woods between Minnesota and Ontario (annual harvest of about 4500 kg; 350 LS) (P. Talmage, MDNR, Baudette, MN, unpubl. data). These fisheries have all been intensively managed over time to produce sustainable harvests.

Table 8
Lake sturgeon commercial (Comm), recreational (Recr), and Tribal/1st Nations (Tribal) fisheries, and harvest estimates by state and province, USA and Canada

State/Province	Comm. harvest	Recr. fishery	Recr. harvest	Tribal harvest	Recent harvest estimates
Alabama	No	No	No	No	
Alberta	No	Yes	No	Yes	
Georgia	No	No	No	No	
Illinois	No	No	No	No	
Indiana	No	No	No	No	
Iowa	No	No	No	No	
Kentucky	No	No	No	No	
Manitoba	No	Yes	No	Yes	
Michigan	No	Yes	Yes	Yes	Anglers on Lake St. Clair reported harvesting 4 legal LS (3% of estimated catch of legal lake sturgeon) in 2007. Tribal fishermen are allowed to take 1–2 incidentally caught LS home for domestic use per year
Minnesota	No	Yes	Yes	No	Registered harvest of 356 LS in 2015 (~8825 lbs)
Missouri	No	No	No	No	
New York	No	No	No	No	
Ohio	No	No	No	No	
Ontario	Yes	Yes	No	Yes	There are First Nation harvests and commercial licenses, but there is no means to keep track on numbers harvested. Estimates of 450–680 kg annual 1st Nation subsistence harvest from Lake of the Woods. Recreational fisheries were closed in 2008 with two exceptions (FMZ 1 and 8 although no harvest allowed)
Pennsylvania	No	No	No	No	,
Quebec	Yes	Yes	Yes	Yes	80 000 kg annual commercial harvest
Saskatchewan	No	Yes	No	Yes	Harvest records before the closure were never obtained.
Tennessee	No	No	No	No	
Wisconsin	No	Yes	Yes	Yes	Spear harvest of 2158 LS (44 000 kg) during 2015 season. Hook and line harvest in 2014 of 37 LS statewide.

References for each State/Province: Alabama (Online at: http://www.outdooralabama.com/lake-sturgeon, accessed 15 January 2016); Alberta (Online at: Alberta Lake Sturgeon Recovery Team (2011); accessed 15 January 2016); Georgia (Online at: http://www.georgiawildlife.com/ Fisheries/LakeSturgeon; accessed 15 January 2015); Illinois (Online at: http://www.dnr.illinois.gov/conservation/NaturalHeritage/Pages/Fish.a spx; accessed 15 January 2016); Indiana (Online at : http://www.eregulations.com/indiana/fishing/fishing-regulations/; accessed 15 January 2016); Iowa (Online at: http://www.iowadnr.gov/idnr/Fishing/Iowa-Fish-Species/Fish-Details/SpeciesCode/LAS; accessed 15 January 2016); Kentucky (Online at: http://fw.ky.gov/Fish/Pages/Lake-Sturgeon.aspx); Manitoba 2012; Michigan (Online at: http://www.eregulations.com/ michigan/fishing/lake-sturgeon-regulations/; accessed 15 January 2016; Towns and Thomas, 2011; P. Schneeberger, MI Department of Natural Resources, Marquette, MI, pers. comm.); Minnesota (Onoine at: http://www.dnr.state.mn.us/fishmn/regs.html; accessed 15 January 2016; Talmage, P., T. Heinrich, D. Topp, K. Peterson. 2009.; Talmage, P., MNDNR, Baudette, MN, pers. comm.); Missouri (Online at: http:// mdc.mo.gov/discover-nature/field-guide/lake-sturgeon; accessed 15 January 2016); New York (Online at: http://www.dec.ny.gov/animals/ 26035.html; accessed 15 January 2016); Ohio (Online at: http://wildlife.ohiodnr.gov/species-and-habitats/species-guide-index/fish/lake-sturge on; accessed 15 January 2016); Ontario (pers. Comm. Haxton, T. Ontario Ministry of Natural Resources, Peterborough, ON); Pennsylvania (Online at: http://www.fish.state.pa.us/pafish/fishhtms/chap5.htm; accessed 15 January 2016); Quebec (Online at: http://www.mffp.gouv.qc.ca/ english/publications/online/wildlife/fishing; accessed 15 January 2016); Mailhot et al., 2011); Saskatchewan (Online at: http://www.environme nt.gov.sk.ca/adx/aspx/adxGetMedia.aspx?DocID = 2556b9d4-9af7-4a52-a5e8-3293cc964159&MediaID = e77ef795-6f4f-41e6-8c2e-6acc21884661&Filename = 2015 + Anglers + Guide.pdf&l = English; accessed 15 January 2016); Tennessee (Online at: http://www.tnfish.org/LakeS turgeonRestoration\_TWRA/AcipenserFulvescensResorationTennessee\_TWRA.htm; accessed 15 January 2016); Wisconsin (Online at: http:// dnr.wi.gov/topic/fishing/sturgeon/SturgeonInlandFishery.html; http://dnr.wi.gov/topic/fishing/sturgeon/SturgeonInlandFishery.html http://dnr. wi.gov/topic/Fishing/Sturgeon/SturgeonLakeWinnebago.html; accessed 15 January 2016); pers. Comm. Koenigs, R. and Scheidegger, K., WI Department of Natural Resources).

## Major anthropogenic habitat impacts

Nearly all sturgeon species are considered at risk due to the combination of overexploitation and habitat degradation (Birstein et al., 1997; Pikitch et al., 2005). Activities including pulp and paper mill effluent, raw sewage discharges and other toxic effluents have all contributed to water pollution and impaired water quality for LS (Mosindy and Rusak, 1991; Dumas et al., 2003; OMNR, 2009; Heinrich and Friday, 2014). Further, environmental degradation in the form of sediment pollution, damming of rivers, destruction of spawning habitat, deterioration of water quality, and siltation occurred throughout the range of LS distribution

(Billard and Lecointre, 2001; Pikitch et al., 2005; Aadland, 2015). Lake Sturgeon are also known to be sensitive to the lampricide TFM (Johnson et al., 1999).

For the most part, LS overexploitation is now controlled with stringent regulations (Rochard et al., 1990) supported by consistent and comprehensive monitoring (Dumont et al., 1987; Bruch, 1999). Therefore, habitat alteration/degradation is now considered to be the greatest remaining threat to LS populations. A study of the different anthropogenic stressors affecting LS in a large regulated river concluded that regardless of historical practices, water power management (i.e., presence and operation of hydroelectric facilities) was now

the factor impeding population recovery the most (Haxton and Findlay, 2009). Similarly, the variation in LS abundance across Ontario was primarily explained by the presence of hydroelectric generating stations (Haxton et al., 2014b). In comparison, LS populations are recovering and/or sustaining viable fisheries in other parts of the LS range despite waterways being fragmented by dams for over 100 year (Scholl, 1986; WDNR, 2000). These observations suggest that dams and sturgeon can co-exist if the correct planning and mitigative techniques are employed (Haxton et al., 2014b; Aadland, 2015).

Dams are often designed and managed to reduce flow variability in the rivers downstream (i.e., provide water when required and reduce peak flows to control flooding) by increasing water level fluctuations in upstream reservoirs (Baxter and Glaude, 1980; Nilsson and Berggren, 2000). As a result, many rivers with the aforementioned regulation strategy have been transformed into a series of storage reservoirs and run-of-the-river impoundments (Nilsson and Berggren, 2000) changing characteristics of the system from lotic to lentic (Nilsson and Berggren, 2000; Friedl and Wuest, 2002). Lake Sturgeon populations can sustain themselves quite well with additional lentic areas on systems created by hydro dams providing adequate spawning and nursery areas are still available in the lotic areas (Barth et al., 2009, 2011).

Lake Sturgeon are migratory with large distances often separating spawning, nursing and overwintering habitats (Harkness and Dymond, 1961; Houston, 1987; Beamesderfer and Farr, 1997; Ferguson and Duckworth, 1997; Baker and Borgeson, 1999; Williot et al., 2002). Dams may form barriers eliminating the upstream movement of fish and fragmenting populations. However, sturgeon can persist in fragmented systems providing adequate habitat is present to the meet the life history requirement (Beamesderfer et al., 1995). Therefore, it is critical for sturgeon management and recovery programs to identify the habitat available in all sections of the river (between dams) and set population objectives that will assist in determining where habitat needs to be developed and/or re-connected. This process can also be used to decide where and how to move LS past dams to meet objectives.

Anadromous species may be unable to migrate for spawning or nursing purposes if insufficient water is passed through the dam to provide adequate habitat downstream for LS populations to successfully complete critical life history requirements (Geen, 1974; Rochard et al., 1990; Liu and Yu, 1992; Mirza and Ericksen, 1996; Cada, 1998; Gehrke et al., 1999; Dudgeon, 2000; Nilsson and Berggren, 2000; Williot et al., 2002). In these cases, flow regimes need to be negotiated and implemented that address agreed upon LS management and/or recovery objectives and balance the need for alternative uses of water with the needs of the LS population.

Dams alter habitat and flood natural rapids that may have been traditionally used for spawning (Zhong and Power, 1996; Nilsson and Berggren, 2000; Aadland, 2015). As mentioned earlier, LS spawn in shallow, fast-moving waters; areas that are usually sites for dam construction because they

are generally areas of greatest hydraulic head. Typically, LS will concentrate below these dams and attempt to spawn on the remaining natural substrate or on substrate that was placed on the river bed through the dam construction process. Regulated flows that disrupt normal spawning patterns (Fernadez-Pasquier, 1999) and diurnal fluctuations in flows that de-water spawning areas leaving their eggs exposed to desiccation (Il'ina and Gordeyev, 1972; Gaboury and Patalas, 1984; Humphries and Lake, 2000) need to be mitigated to ensure adequate flows are maintained through the spawning, incubation, and larval swim-up periods for LS.

Drastic and rapid changes in flows or water levels may affect downstream passage of many individuals and cause entrainment or entrapment in less than ideal conditions (Geen, 1974; Cada, 1998; Pringle et al., 2000). Entrainment may artificially increase mortality of spawning fish, which ultimately could impact future spawning stocks (especially species with traditionally low adult mortality). The migratory nature of LS makes them prone to entrainment (McKinley et al., 1998; McDougall et al., 2013, 2014). In northern Ontario, LS have been entrained during the operation of Adam's Creek sluice gates and became stranded in pools downstream during de-watering (Seyler et al., 1996; Sheehan, 2001). The remotely controlled sluice gates are operated to pass water down a diversion during excessive flow and has a discharge capacity of 4970 m<sup>3</sup> s<sup>-1</sup> (Sheehan, 2001). Lake Sturgeon from upstream reaches (Little Long Headpond) have been entrained during their post spawning migration, and while many LS were observed to sustain extensive injuries, tagging projects suggested that not all injuries were fatal. A relocation project moving LS stranded in pools back into Little Long Headpond has been implemented until such times that entrainment can be prevented (Seyler et al., 1996; Sheehan, 2001). During the period from 1990 to 2000, approximately 3500 LS were relocated representing approximately 14% of the population (Sheehan, 2001). Entrainment at this location is still an issue since 472 and 226 LS required relocation in 2007 and 2008 respectively (Barbour, D. OMNR, Kapuskasing, ON, pers. comm.). The numbers relocated does not account or reflect the LS that died during stranding or washed downstream from the high flows.

If appropriate measures are not taken (i.e. effective trash rack spacing on turbine inflow bays), entrainment through hydro-electric stations can result in turbine mortality of subadult and adult LS. Several LS carcasses with obvious blade strikes were located immediately downstream of a hydro-electric facility during an American Eel (*Anguilla rostrata*) turbine mortality study (Bendig, A. OMNR, Kemptville, ON, pers. comm.). However, young sturgeon can survive entrainment quite well, especially if it occurs through the sluicegates at the facilities (McDougall et al., 2014). Fingerling and yearling size LS were shown to have exceptionally high survival (>90%) passing through turbines in a recent experiment conducted on the Wolf River in Wisconsin (R. Koenigs, WDNR, Oshkosh, WI, unpubl. data).

Dredging is a major problem in many of the Great Lakes connecting waters and in large rivers (Beamesderfer and Farr, 1997; Auer, 2003). Dredging activities can remove spawning habitat and underwater cover required by LS (e.g.,

Caswell et al., 2004; Nilo et al., 2006) or depauperate LS prey through deposition of material on nursery areas (Gerig et al., 2011). Dredging can also increase turbidity, reduce light penetration and decrease levels of dissolved oxygen. Due to their relatively poor swimming abilities and benthic orientation, juvenile sturgeon can also be entrained during dredging activities (Veshchev, 1981; Boysen and Hoover, 2009).

#### Other stochastic natural impacts

Lake Sturgeon, along with other sturgeon species, have evolved very efficient and effective life history strategies for dealing with the inherent stochasticity of natural systems. Animals that are short-lived, small-sized and early-maturing have been classified as *r*-strategists (*r*, the intrinsic rate of population increase), whereas animals like sturgeon that are long-lived, large-sized, very fecund, and late-maturating are *K*-strategists (*K*, the carrying capacity of a species in a particular population) also known as periodic strategists (Pianka, 1970; Winemiller and Rose, 1992).

Natural appearing cycles in abundance of animals are commonly observed with various species of animals (Zimmerman et al., 2008), but these cycles are often exacerbated or exaggerated by human exploitation or human caused habitat alterations. Stock recruitment dynamics, other population factors, and naturally cycling environmental factors will affect the cycling of abundance as well. LS, even as periodic life history strategists, would not necessarily be immune to being impacted by natural stochastic factors which ultimately could cause local or regional populations to cycle.

Bruch's (2008) stochastic simulation modeling results suggest LS may experience natural cycling of abundance in the Winnebago System. With a Ricker stock–recruit relationship (the best fit S-R model for the Winnebago data) and an annual conditional natural mortality rate of 5.4%, adult females were predicted to naturally cycle from high abundance to low abundance every 28 years. Further, the average level of abundance over the long-term was dependent upon the level of exploitation. The model indicated that recruitment was increasing in the early 2000s, but that the adult stock was moving towards the next low point predicted to occur around the year 2034, which was then followed by a high point of abundance in approximately 2062. Model outputs suggested cycling of abundance to be consistent over the 500 years that were simulated.

# Emerging impacts, threats and risks

Likely the greatest emerging threat to LS throughout their range, aside from the renewal of overexploitation, any further loss of habitat, an outbreak of a new detrimental disease or parasite, and/or some other unforeseen natural or manmade disaster, would be the loss of interest on the part of the public and politicians. This interest is key to the financial support needed to fund management, recovery, research, and habitat programs and LS programs would be set back 50 or more years without this interest. Maintaining this support is challenging given the long term nature of sturgeon recovery

and the relatively high costs for sturgeon aquaculture, monitoring, research, and habitat development. While maintaining public interest in sturgeon programs is key to maintaining financial and political support for programs, keys to maintaining public interest are pro-active meaningful public involvement programs that engage and interest people in LS. Interest that, where possible, can be spurred by the hope of participating someday in recreational fisheries for restored LS populations, even if the fisheries are non-harvest catch and release only. The fishing licenses sold in Wisconsin, Michigan, and Minnesota are exemplary examples that a licence system can produce revenues that can go a long way to keeping LS management and recovery programs in business for many, many years. Engaging the public from the ground-up in the development of recovered LS populations and fisheries that will ultimately be created builds public ownership in the program and helps ensure long term program funding.

#### Population recovery actions

Lake Sturgeon restoration efforts through stocking and habitat improvements have been ongoing in several jurisdictions since the early 1980s. Pioneering efforts to artificially propagate lake sturgeon can be traced back as early as 1919 in Ontario (Harkness and Dymond, 1961; Kerr, 2006), however were unsuccessful as effective methods were not honed until the late 1970s (Czeskleba et al., 1985; Smith and Hobden, 2011). LS habitat development, specifically spawning habitat, has been occurring unintentionally and intentionally for over 50 year.

The placement of riprap in LS river systems to stabilize river banks and beds, and as part of the process of dam construction and maintenance has created many new areas for LS to spawn in areas on rivers where in many cases LS had previously never spawned (K. Koenigs, WDNR, Oshkosh, WI, unpubl. Data, 2000; Bruch and Binkowski, 2002). Lake sturgeon favoured a spawning site constructed downstream of the Carillon Dam on the Ottawa River for American Shad (*Alosa sapidissima*) (Rochard et al., 1990). The success of the man-made LS spawning sites created through riprap projects inspired other even larger scale successful spawning rehabilitation sites such as those built in Des Praires River (Quebec Canada) (Dumont et al., 2011) and on the Detroit River system in Michigan (Roseman et al., 2011).

Successful population re-establishment through stocking has been documented in numerous watersheds with successful natural reproduction from stocked fish occurring in the Mississippi River, Missouri (Moore, T., Missouri Department of Conservation, Hannibal, MO, pers. comm.), and in St. Louis River, Wisconsin/Minnesota (Margenau, T., WDNR, Bayfield, WI, pers. comm.).

While most LS restoration efforts have relied primarily on stocking and habitat management or development, which requires 35–40 year of effort to show initial success of natural reproduction, a recent effort to restore a LS population in Wisconsin without stocking or habitat alterations has resulted in successful natural reproduction of a newly created spawning stock within 1 year of initial work. A capture and

transfer program initiated on the Wolf River in fall 2011 aimed to restore LS spawning activity to two upstream sections of the river where spawning had been absent for 50-100 years, while also establishing a local resident LS population. Both objectives were achieved within the first few years, with spawning activity observed in the first year, following fish transfer and progeny from the transferred adults captured following observed spawning of the transferred fish in the 2nd year. Fish were captured and transferred from downstream sections of the river where a natural population exists to a section of the river above two dams that have prevented movement of spawning fish into this section of river since the early 1900s. Aquatic invasive species issues on the river currently prevent volitional movement of fish upriver which complicates efforts for considering the installation of fish passage at the two dams bypassed by capture and transfer operations (Koenigs, R., WNDR, Oshkosh, WI, unpubl. data).

### Recovery monitoring and timeline predictions

Based on results cited above from restoration efforts in Missouri Wisconsin, and Wisconsin/Minnesota boundary waters, LS recovery appears to be very achievable and assessable. Time and patience (in addition to consistent funding) are of course essential elements in any recovery program, especially in programs that are attempting to rebuild sturgeon stocks from scratch through stocking or from low remnant levels through natural recovery. A substantial time element is also required for recovery being pursued through adult capture and transfer, but with LS a time savings of 30–35 years may be enjoyed using this method if an adequate donor population is available. Overall based on the 35+ years of experience and initial findings from these recovery efforts a recovery timeline (starting with remnant stock of 0–200 adults) could potentially consist of:

If using stocking of fingerlings or yearlings as the primary recovery tool:

- 1st 30-50 years stocking annually to rebuild adult spawning stock; sources have been from local hatcheries and from streamside rearing units; "head starting" or raising captured wild larvae in a hatchery for a time before release to minimize mortality has also been used on some recovery waters (Peterson et al., 2007); all fish stocked should be permanently marked (PIT tag or other effective permanent mark); target adult densities should be estimated and stocking calibrated over time once tag returns and abundance estimates of stocked year classes in assessments provide an indication of survival/mortality rates; tag return rates of young fish that can be accurately aged will provide measure of any natural recruitment occurring during rebuilding period. Habitat improvements (if needed) should be made where possible during this period anticipating ultimate use by new sturgeon stock.
- 2nd 30–50 years no stocking; focus on assessment of stocked (and existing natural) fish for distribution, densities, growth, mortality, natural recruitment.

If using 'Capture and Transfer' of adults as the primary recovery tool:

- 1st 10 years— set long term density and distribution goals for new population being created by transferred fish; capture and transfer optimum minimum of 100 adults (30 gravid females and 70 gravid males optimum) per year; monitor post transfer behavior, movement, spawning activity (telemeter released fish during first 3 years of transfers— track long term; PIT tag all released fish), and spawning success. Habitat improvements (if needed) should be made where possible during this period anticipating ultimate use by new sturgeon stock.
- 2nd 10 years calibrate capture and transfer numbers and final transfer timeline based on distribution, density, spawning and larval assessments of fish transferred in previous 10 years.

If using natural recovery of remnant stock assuming some (100–200) remnant adults remain within the target recovery area:

- 1st 50–100 years monitor densities (relative or absolute), and spawning activity/success of remnant stock. Improve habitat where needed and possible.
- 2nd 50 years initiate stocking or adult capture and transfer if no signs of natural recovery are evident. If some recovery signs are evident, continue to monitor.

# Research needs - priority data gaps

- 1 Document success or failure of ongoing long-term LS recovery methods and efforts.
- 2 Develop/Update the best management practices for conservation genetics, gamete collection strategies, rearing strategies, and stocking strategies.
- 3 Determine distribution, habitat selectivity, and movement of juvenile and subadult LS, as well as the variability in this behavior across the wide range of waters inhabited by LS in North America
- 4 Implement genomic approaches to studying and conserving genetic diversity in an effort to better manage for *adaptive* genetic variation
- 5 Determine on a case by case basis when and where fish passage is needed for LS on fragmented systems and develop technology and/or methods to facilitate/ensure upstream and downstream movement of LS at targeted dams and hydroelectric facilities.
- **6** Evaluate fish passage facilities for effectiveness to guide design, and optimize efficiencies of future facilities.
- 7 Document effectiveness of current strategies and methods designed to create or enhance LS habitat as well as mitigate negative impacts of various anthropogenic activities on sturgeon habitat.

#### Current prognosis for species

Lake Sturgeon is one of two Acipenseriformes listed as 'least concern' by IUCN's Redlist (http://www.iucnredlist.org/)

with the other of the 24 species listed with some kind of status be it 'threatened', 'critically endangered' etc. in the wild. As detailed in the 'Distribution and general abundance' section, many robust populations remain. In addition, the status of LS population is unknown in many northern Ontario and Quebec waterbodies. Lake Sturgeon, as with other Acipenseriformes, are gaining notoriety. Attention has been refocused on this species. Therefore, greater efforts have been concentrated at determining science needs and recovery efforts (Peterson et al., 2007). However, the current demand for renewable energy and subsequent development of many northern rivers for hydro-electric purposes will add pressure to these remote, pristine populations. Some robust populations, for example the Winnebago Lake system in Wisconsin and St. Lawrence River in Quebec are excellent models that show, through aggressive and pro-active management, that populations can be maintained a high levels and can be sustainably harvested through commercial or recreational fisheries (Dumont et al., 1987; Bruch, 1999; Mailhot et al., 2011).

Overall, LS populations today enjoy much greater protection from over-exploitation and have greater opportunities for recovery and sustainability throughout their range than they have experienced for more than a century. A combination of factors including: increased attention over the last 30-40 years by state and provincial governments to effectively manage harvest and conduct proper assessments, increased public awareness of LS and their extreme vulnerability to overexploitation, improvements in assessment techniques, improvement in LS propagation techniques and stocking strategies, exponential expansion of population studies and research, increasing awareness and efforts to improve habitat and water quality, and the formation of the North American Sturgeon and Paddlefish and World Sturgeon Conservation Societies have all contributed to greater protection and recovery potential. While these are all positive steps that collectively should allow many LS populations to continue or start down the road to recovery, there are still waters and populations that may not be getting the attention needed to allow their recovery to occur. Generally, though, things are better now than they were 30 years ago for LS across the landscape of North America and, for the most part, things are moving in a positive direction.

#### Acknowledgements

We would like to acknowledge Drs. Doug Peterson, Paul Vecsei, and Cecil Jennings, as well as the publisher Springer, for their generous permission to reproduce an excerpt and four figures on general morphology of Lake Sturgeon from their review paper Peterson, D. L.; Vecsei, P.; Jennings, C., 2007: Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Rev. Fish Biol. Fisher. 17, 59–76. We also would like to acknowledge the very helpful contributions made by Dr. Anindo Choudhury to the 'Diseases and parasites' section of the manuscript.

#### References

- Aadland, L., 2015: Barrier effects on native fishes of Minnesota. Minnesota Department of Natural Resources, St. Paul, MN, USA, 34 pp.
- Adams, W. E., Jr; Kallemeym, L. W.; Willis, D. W., 2006: Lake sturgeon population characteristics in Rainy Lake, Minnesota and Ontario. J. Appl. Ichthyol. 22, 97–102.
- Alberta Lake Sturgeon Recovery Team, 2011: Alberta Lake Sturgeon Recovery Plan, 2011–2016. Alberta Environmental and Sustainable Resource Development, Alberta Species at Risk Recovery Plan No. 22, Edmonton, AB, Canada, 98 pp.
- Altenritter, M. E. L.; Wieten, A. C.; Ruetz, C. R., III; Smtih, K. M., 2013: Seasonal spatial distribution of juvenile lake sturgeon in Muskegon Lake, Michigan, USA. Ecol. Freshw. Fish 22, 467– 478
- Artyukhin, E. N., 1995: On biogeography and relationships within the genus *Acipenser*. Sturg. Quart. 3, 6–8.
- Auer, N. A., 1996a: Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. Can. J. Fish Aquat. Sci. 53(Suppl. 1), 152–160.
- Auer, N. A., 1996b: Responses of spawning lake sturgeon to change in hydroelectric facility operation. Trans. Am. Fish. Soc. 125, 66–77.
- Auer, N., 1999a: Lake sturgeon: a unique and imperiled species in the Great Lakes. In: Great Lakes Fisheries Policy and Management: a binational perspective. W. W. Tayler, C. P. Ferreri (Eds). Michigan State University Press, East Lansing, MI, USA, pp. 515–536.
- Auer, N., 1999b: Population characteristics and movements of lake sturgeon in the Sturgeon River and Lake Superior. J. Great Lakes Res. 25, 282–293.
- Auer, N. A., 2003: Lake sturgeon rehabilitation plan. Great Lake Fisheries Commission, Ann Arbor, MI, USA, 28 pp.
- Auer, N. A.; Baker, E. A., 2002: Duration and drift of larval lake sturgeon in the Sturgeon River, Michigan. J. Appl. Ichthyol. 18, 557–564.
- Bajkov, A., 1930: Fishing industry and fisheries investigations in the prairie provinces. Trans. Am. Fish. Soc. 60, 215–237.
- Baker, J. P., 1980: The distribution, ecology, and management of the lake sturgeon (Acipenser fulvescens Rafinesque) in Michigan. Fisheries Research Report No. 1883. Michigan Department of Natural Resources, Fisheries Division, USA, 95 pp.
- Baker, J. P., 1982: Yield per recruit of inland stocks of lake sturgeon (Acipenser fulvescens Raf.) in Michigan. Mich. Acad., 19(4), 415–425.
- Baker, E. A., 2006: Lake sturgeon distribution and status in Michigan, 1996–2005. Fisheries Technical Report 2006–4. Michigan Department of Natural Resources, Marquette, MI, USA, 17 pp.
- Baker, E.; Borgeson, D., 1999: Lake sturgeon abundance and harvest in Black Lake, Michigan, 1975–1999. N. Am. J. Fish. Manage. 19, 1080–1088.
- Barth, C. C.; Peake, S. J.; Allen, P. J.; Anderson, W. G., 2009: Habitat utilization of juvenile lake sturgeon, *Acipenser fulvescens*, in a large Canadian river. J. Appl. Ichthyol. **25**(Suppl. 2), 18–26.
- Barth, C. C.; Anderson, W. G.; Henderson, L. M.; Peake, S. J., 2011: Home range size and seasonal movements of juvenile lake sturgeon in a large river in the Hudson Bay drainage basin. Trans. Am. Fish. Soc. 140, 1629–1641.
- Baxter, R. M.; Glaude, P., 1980: Environmental effects of dams and impoundments in Canada: experience and prospects. Can. B. Fish. Aquat. Sci. 205, 40.
- von Bayer, H., 1910: A method of measuring fish eggs. Bull. US Bur. Fisheries 28, 1009–1014.
- Beamesderfer, R. C. P.; Farr, R. A., 1997: Alternatives for the protection and restoration of sturgeons and their habitat. Environ. Biol. Fish. 48, 407–417.
- Beamesderfer, R. C. P.; Rien, T. A.; Nigro, A. A., 1995: Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the Lower Columbia River. Trans. Am. Fish. Soc. 124(6), 857–872.

Beamish, F. W. H.; Noakes, D. L. G.; Rossiter, A., 1998: Feeding ecology of juvenile lake sturgeon, *Acipenser fulvescens*, in northern Ontario. Can. Field Nat. 112, 459–468.

- Bemis, W. E.; Findeis, E. K., 1994: The sturgeons' plight. Nature 370, 602.
- Bemis, W. E.; Kynard, B., 1997: Sturgeon rivers: an introduction to acipensiform biogeography and life history. Environ. Biol. Fish. 48, 167–183
- Bemis, W. E.; Findeis, E. K.; Grande, L., 1997: An overview of Acipenseriformes. Environ. Biol. Fish. 48, 25–71.
- Benson, A. C.; Sutton, T. M.; Elliott, R. F.; Meronek, T. G., 2005: Seasonal movement patterns and habitat preferences of age-0 lake sturgeon in the Lower Peshtigo River, Wisconsin. Trans. Am. Fish. Soc. 134, 1400-1409.
- Billard, R.; Lecointre, G., 2001: Biology and conservation of sturgeon and paddlefish. Rev. Fish Biol. Fisher. 10, 355–392.
- Birstein, V. J.; Bemis, W. E.; Waldman, J. R., 1997: The threatened status of acipenseriform species: a summary. Environ. Biol. Fish. 48, 427–435.
- Birstein, V. J.; Doukakis, P.; DeSalle, R., 2002: Molecular phylogeny of Acipenseridae: nonmonophyl of Scaphirynchidae. Copeia 2002(2), 287–301.
- Blacklidge, K. H.; Bidwell, C. A., 1993: Three ploidy levels indicated by genome quantification in Acipenseriformes of North America. J. Hered. 84, 427–430.
- Bocast, C.; Bruch, R. M.; Koenigs, R., 2014: Sound production of spawning lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in the Lake Winnebago watershed, Wisconsin, USA. J. Appl. Ichthyol. 30, 1186–1194.
- Boiko, N. E., 1993: Olfactory imprinting in young sturgeon.
   Abstract 8. International Symposium of Sturgeon. September 6–11, 1993. VNIRO Publishers, Moscow, Russia.
- Borkholder, B. D.; Morse, S. D.; Weaver, H. T.; Hugill, R.; Linder, A. T.; Schwarzkopf, L. M.; Perrault, T. E.; Zacher, M. J.; Frank, J. A., 2002: Evidence of a year-round resident population of lake sturgeon in the Kettle River, Minnesota, based on radio telemetry and tagging. N. Am. J. Fish. Manage. 22, 888–894.
- Bott, K.; Kornely, G. W.; Donofrio, M. C.; Elliott, R. F.; Scribner, K. T., 2009: Mixed-stock analysis of lake sturgeon in the Menominee River sport harvest and adjoining waters of Lake Michigan. N. Am. J. Fish. Manage. 29, 1636–1643.
- Boysen, K. A.; Hoover, J. J., 2009: Swimming performance of juvenile white sturgeon (*Acipenser transmontanus*): training and the probability of entrainment due to dredging. J. Appl. Ichthyol. **25**(Suppl. 2), 54–59.
- Brennen, J. S.; Caillet, G. M., 1989: Comparative age-determination techniques for white sturgeon in California. Trans. Am. Fish. Soc. 118, 296–310.
- Brown, J. R.; Beckenbach, K.; Beckenbach, A. T.; Smith, M. J., 1996: Length variation, heteroplasmy and sequence divergence in the mitochondrial DNA of four species of sturgeon (*Acipen-ser*). Genetics 142, 525–535.
- Bruch, R. M., 1999: Management of lake sturgeon in the Winnebago System – long term impacts of harvest and regulations on population structure. J. Appl. Ichthyol. 15, 142–152.
- Bruch, R. M., 2008: Modeling the population dynamics and sustainability of lake sturgeon in the Winnebago System, Wisconsin. PhD Dissertation. University of Wisconsin-Milwaukee, Milwaukee, WI, USA, 269 pp.
- Bruch, R. M.; Binkowski, F. P., 2002: Spawning behaviour of lake sturgeon (Acipenser fulvescens). J. Appl. Ichthyol. 18, 570-579
- Bruch, R. M.; Dick, T.; Choudhury, A., 2001: A Field Guide for the Identification of Stages of Gonad Development in Lake Sturgeon, Acipenser fulvescens Rafinesque, with notes on lake sturgeon reproductive biology and management implications. WI Dept. Nat. Res. Oshkosh and Sturgeon for Tomorrow publication. Graphic Communications Center, Inc. Publisher, Appleton, WI, USA, 38 pp.

Bruch, R. M.; Miller, G. L.; Hansen, M. J., 2007: Fecundity of Lake Sturgeon (*Acipenser fulvescens*, Rafinesque) in Lake Winnebago, Wisconsin, USA. J. Appl. Ichthyol. **22**(Suppl. 1), 116–118.

- Bruch, R. M.; Campana, S. E.; Davis-Foust, S. L.; Hansen, M. J.; Janssen, J., 2009: Age validation of lake sturgeon using bomb radiocarbon and known age fish. Trans. Am. Fish. Soc. 138, 361–371.
- Bruch, R. M.; Kamke, K.; Haxton, T., 2011: Use of a modified form factor to compare condition among North American lake sturgeon stocks. J. Appl. Ichthyol. 27(Suppl. 2), 34–40.
- Buddington, R. K.; Christofferson, J. P., 1985: Digestive and feeding characteristics of the chondrosteans. Environ. Biol. Fish 14, 31–41.
- Cada, G. F., 1998: Efforts to reduce the impacts of hydroelectric power production on reservoir fisheries in the United States. Int. Rev. Hydrobiol. 83, 43–50.
- Caroffino, D. C.; Sutton, T. M.; Lindberg, M. S., 2009: Abundance and movement patterns of age-0 juvenile lake sturgeon in the Peshtigo River, Wisconsin. Environ. Biol. Fish. 86, 411–422.
- Caroffino, D. C.; Sutton, T. M.; Elliott, R. F.; Donofrio, M. C., 2010: Early life stage mortality rates of Lake Sturgeon in the Peshtigo River, Wisconsin. N. Am. J. Fish. Manage., 30(1), 295–304.
- Caswell, N. M.; Peterson, D. L.; Manny, B. A.; Kennedy, G. W., 2004: Spawning by lake sturgeon (*Acipenser fulvescens*) in the Detroit River. J. Appl. Ichthyol. **20**, 1–6.
- Cech, J. J.; Doroshov, S. I., 2004: Environmental requirements, preferences and tolerance limits of North American sturgeons. In: Sturgeons and Paddlefish of North America. G. T. O. LeBreton, F. W. H. Beamish, R. S. McKinley (Eds). Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 73–86.
  Chiasson, W. B.; Noakes, D. L. G.; Beamish, F. W. H., 1997: Habi-
- Chiasson, W. B.; Noakes, D. L. G.; Beamish, F. W. H., 1997: Habitat, benthic prey, and distribution of juvenile lake sturgeon (*Acipenser fulvescens*) in northern Ontario rivers. Can. J. Fish Aquat. Sci. 54, 2866–2871.
- Chiotti, J. A.; Holtgren, J. M.; Auer, N. A.; Ogren, S. A., 2008: Lake sturgeon spawning habitat in the Big Manistee River, Michigan. N. Am. J. Fish. Manage. 28, 1009–1019.
- Choudhury, A., 2009: A new deropristiid species (Trematoda: Deropristiidae) from the Lake Sturgeon Acipenser fulvescens in Wisconsin, and its biogeographical implications. J. Parasitol. 95(5), 1159–1164.
- Choudhury, A.; Dick, T. A., 1991: Parasites of lake sturgeon, *Acipenser fulvescens* (Chondrostei: Acipenseridae), with special reference to the coelenterate parasite, *Polypodium hydriforme*. In: Acipenseriform fishes: an annotated bibliography. Can. Tech. Rep. Fish. Aquat. Sci., 1772, 15 pp.
- Choudhury, A.; Dick, T. A., 1992: Spinitectus acipenseri n. sp. (Nematoda: Cystidicolidae) from the lake sturgeon Acipenser fulvescens Rafinesque in Canada. Syst. Parasitol., 22, 131–140.
- Choudhury, A.; Dick, T. A., 1993: Parasites of lake sturgeon, Acipenser fulvescens, Rafinesque, 1817 (Chondrostei: Acipenseridae), from central Canada. J. Fish Biol. 42, 571–584.
- Choudhury, A.; Dick, T. A., 1998a: The historical biogeography of sturgeons (Osteichthyes: Acipenseridae): a synthesis of phylogenetics, palaeontology and palaeogeography. J. Biogeogr. 25, 623–640.
- Choudhury, A.; Dick, T. A., 1998b: Patterns and determinants of helminth communities in sturgeons (Chondrostei: Acipenseridae) with special reference to the lake sturgeon, *Acipenser fulvescens*. Can. J. Zool., 76, 330–349.
- Choudhury, A.; Dick, T. A., 2001: Sturgeons and their parasites: patterns and processes in historical biogeography. J. Biogeogr., 28, 1411–1439.
- Choudhury, A.; Bruch, R. M.; Dick, T. A., 1996: Helminths and food habits of the lake sturgeon, *Acipenser fulvescens*, from Lake Winnebago, Wisconsin. Am. Midl. Nat., **135**, 274–282.
- Craig, J. M.; Thomas, M. V.; Nichols, S. J., 2005: Length-weight relationship and a relative condition factor equation for lake sturgeon (*Acipenser fulvescens*) from the St. Clair River system (Michigan, USA). J. Appl. Ichthyol. **21**, 81–85.

- Cuerrier, J. P., 1949: Observations sur l'esturgeon de lac (Acipenser fulvescens Raf.) dans la région du lac Saint-Pierre au cours de la période du frai. Thèse Manuscrit. Université de Montréal, Montréal, Canada. (Original data referenced in Harkness and Dymond, 1961).
- Cuerrier, J. P., 1966: L'esturgeon de lac Acipenser fulvescens Raf. De la region du lac Saint-Pierre au cours de la période du frai. Nat. Can. 94, 279–334.
- Cuerrier, J. P.; Roussow, G., 1951: Age and growth of Lake Sturgeon from Lake St. Francis, St. Lawrence River. Report on material collected in 1947. Can. Fish Cult. 10, 17–29.
- Czeskleba, D. G.; AveLallemant, S.; Thuemler, T., 1985: Artificial spawning and rearing of lake sturgeon, Acipenser fulvescens, in Wild Rose State Fish Hatchery, Wisconsin, 1982–1983. In: North American sturgeons. F. Binkowski, S. I. Doroshov (Eds). Dr. W. Junk Publishers, Dordrecht, The Netherlands, pp. 79–86
- Dadswell, M. J., 1979: Biology and population characteristics of the shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818 (Osteichthyes: Acipenseridae), in Saint John Estuary, New Brunswick, Canada. Can. J. Zool. 57, 2186–2210.
- D'Amours, J.; Thiboudeau, S.; Fortin, R., 2001: Comparison of lake sturgeon (*Acipenser fulvescens*), *Stizostedion* spp., *Castostomus* spp., *Moxostoma* spp., quillback (*Carpiodes cyprinus*) and mooneye (*Hiodon tergisus*) larval drift in Des Prairies River, Quebec. Can. J. Zool. **79**, 1472–1489.
- Daugherty, D. J.; Sutton, T. M.; Elliott, R. F., 2008: Potential for re-introduction of lake sturgeon in five northern Lake Michigan tributaries: a habitat suitability perspective. Aquat. Conserv., 18 (5), 692–702.
- DeHaan, P. W.; Libants, S. V.; Elliott, R. F.; Scribner, K. T., 2006: Genetic population structure of remnant lake sturgeon populations in the Upper Great Lakes basin. Trans. Am. Fish. Soc. 135, 1478–1492.
- Desloges, S.; Cote, C.; Rive, A.; Philips, S.; Deer, J.; Giroux, B.; de Clerk, K.; Dumont, P., 2004: Search for and characterization of lake sturgeon (Acipenser fulvescens) spawning grounds in the upstream portion of the Lachine Rapids (St. Lawrence River) in 2003. Technical Report 16-20E. Québec Ministère des Ressources naturelles, Longueuil, QC, Canada, 48 pp.
- DeVore, J. D.; James, B. W.; Tracey, C. T.; Hale, D. A., 1995: Dynamics and potential production of white sturgeon in the unimpounded lower Columbia River. Trans. Am. Fish. Soc. 124, 845–856.
- Dick, T. A.; Campbell, R. R.; Mandrak, N. E.; Cudmore, B.; Reist, J. D.; Rice, J.; Bentzen, P.; Dumont, P., 2006: Update COSEWIC status report on the lake sturgeon (*Acipenser fulvescens*). Canadian Wildlife Service, Environment Canada, Ottawa, ON, Canada, 107 pp.
- Drauch, A. M.; Fisher, B. E.; Latch, E. K.; Fike, J. A.; Rhodes, O. E., Jr, 2008: Evaluation of a remnant lake sturgeon population's utility as a source for reintroductions in the Ohio River system. Conserv. Genet. 9, 1195–1209.
- Dubreuil, R.; Cuerrier, J. P., 1950: Rapport sur l'étude du cycle de maturation des glandes génitales chez l'esturgeon de lac (*A. fulvescens* Raf.) de la rivière Ottawa, 1949. Ministère d'Industrie et Commerce, Québec et Conseil National de Recherches, Ottawa. Dactylogramme, Kemptville, ON, Canada, 63 pp.
- Dudgeon, D., 2000: Large-scale hydrological changes in tropical Asia: prospects for riverine diversity. Bioscience 50, 793–806.
- Dumas, R.; Trépanier, T.; Simkonequ, M., 2003: Fish problems and partnership solutions: the lake sturgeon case in the L'Assomption watershed. Presentation at the133rd Annual Meeting of the American Fisheries Society. August 10-014, 2003. Québec City, QC, Canada.
- Dumont, P.; Fortin, R.; Desjardins, G.; Bernard, M., 1987: Biology and exploitation of lake sturgeon (*Acipenser fulvescens*) in the Quebec waters of the Saint-Laurent River. In: Proceedings of a workshop on the lake sturgeon (*Acipenser fulvescens*). C. H.

- Oliver (Ed.). Ontario Ministry of Natural Resources, Ontario Fisheries Technical Report Series No 23, pp. 57–76.
- Dumont, P.; D'Amours, J.; Thibodeau, S.; Dubuc, N.; Verdon, R.; Garceau, S.; Bilodeau, P.; Mailhot, Y.; Fortin, R., 2011: Effects of the development of a newly created spawning ground in the Des Prairies River (Quebec, Canada) on the reproductive success of lake sturgeon (*Acipenser fulvescens*). J. Appl. Ichthyol. 27, 394–404.
- Dynesius, M.; Nilsson, C., 1994: Fragmentation and flow regulation of river in systems the northern third of the world. Science **266**, 753–762
- Earle, S., 2002: Status of the lake sturgeon (*Acipenser fulvescens*) in Alberta. Alberta Wildlife Status Report No. 46. Alberta sustainable Resource Development, Calgary, AB, Canada, 32 pp.
- Ebener, M. P.; Bence, J. R.; Newman, K.; Schneeberger, P., 2005: Application of SCAA models to assess lake whitefish stocks in the 1836 treaty-ceded waters of the upper Great Lakes. In: Proceedings of a workshop on the dynamics of lake whitefish (Coregonus clupeaformis) and the amphipod Dioporeia spp. In the Great Lakes. Great Lakes Fishery Commission Report 66, pp. 279–301.
- Ecologistics Limited, 1987: A lake sturgeon yield study on the Kenogami River, Year 3-Phase 1 Report. Prepared for the Ontario Ministry of Natural Resources, Geraldton District. Project Director: A. Sandilands. March 1987, 57 pp.
- Ferguson, M. M.; Duckworth, G. A., 1997: The status and distribution of lake sturgeon (*Acipenser fulvescens*) in the Canadian provinces of Manitoba, Ontario, and Quebec: a genetic perspective. Environ. Biol. Fish. **48**, 299–309.
- Fernadez-Pasquier, V., 1999: *Acipenser sturio* L. in the Guadalquivir river, Spain. Water regulation and fishery as factors in stock decline from 1932 to 1967. J. Appl. Ichthyol. **15**, 133–135.
- Folz, D. J.; Meyers, L. S., 1985: Management of the lake sturgeon (Acipenser fulvescens) population in the Lake Winnebago system, Wisconsin. In: North American sturgeons. F. Binkowski, S. I. Doroshov (Eds). Dr. W. Junk Publishers, Dordrecht, The Netherlands, pp. 135–146.
- Fontana, F.; Bruch, R. M.; Binkowski, F. P.; Lanfredi, M.; Chicca, M.; Beltrami, N.; Conjiu, L., 2004: Karyotype characterization of the lake sturgeon, *Acipenser fulvescens* (Rafinesque 1817) by chromosome banding and fluorescent in situ hybridization. Genome 47, 742–746.
- Forsythe, P. S.; Crossman, J. A.; Bello, N. M.; Baker, E. A.; Scribner, K. T., 2012: Individual-based analyses reveal high repeatability in timing and location of reproduction in lake sturgeon (*Acipenser fulvescens*). Can. J. Fish Aquat. Sci. **69**, 60–72.
- Fortin, R.; Guénette, S.; Dumont, P., 1992: Biologie, exploitation, modélisation et gestion des populations d'Esturgeon jaune (*Acipenser fulvescens*) dans 14 réseaux de lacs et de riviéres du Québec. Québec, Ministére du Loisir, de la Chasse et de la Pêche, Service de l'aménagement et de l'exploitation de la faune et Service de la faune aquatique, Montréal et Québec, Xxi + 213 pp.
- Fortin, R.; Mongeau, J. R.; Desjardins, G.; Dumont, P., 1993: Movements and biological statistics of lake sturgeon (*Acipenser fulvescens*) populations from the St. Lawrence and Ottawa River system, Quebec. Can. J. Zool. 71, 638–650.
- Friday, M. J., 2006: The migratory and reproductive response of spawning lake sturgeon to controlled flows over Kakabeka Falls on the Kaministiquia River, ON 2006. Ontario ministry of Natural Resources Upper Great Lakes Management Unit, Lake Superior QUIK report 06.02. Rosslyn, ON, Canada, 13 pp.
- Friedl, G.; Wuest, A., 2002: Disrupting the biochemical cycles consequences of damming. Aquat. Sci. 64, 55–65.
- Froese, R.; Binohlan, C., 2000: Empirical relationships to estimate asymptotic length, length at first maturity, and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. J. Fish Biol. **56**, 758–773.

Gaboury, M. N.; Patalas, J. W., 1984: Influence of water level drawdown on the fish populations of Cross Lake, Manitoba. Can. J. Fish Aquat. Sci. 41, 118–125.

- Galarowicz, T., 2003: Conservation assessment for lake sturgeon (*Acipenser fulvescens*). USDA Forest Service, Mount Pleasant, MI, USA, 24 pp.
- Geen, G. H., 1974: Effects of hydroelectric development in western Canada on aquatic ecosystems. J. Fish. Res. Bd. Can. 31, 913– 927
- Gehrke, P. C.; Astles, K. L.; Harris, J. H., 1999: Within-catchment effects of flow alteration on fish assemblages in the Hawkesbury-Nepean river system, Australia. Regul. River. 15, 181–198
- Gerig, B.; Moerke, A.; Greil, R.; Koproski, S., 2011: Movement patterns and habitat characteristics of lake sturgeon (*Acipenser fulvescens*) in the St. Marys River, Michigan, 2007–2008. J. Great Lakes Res. 37, 54–60.
- Hale, M. C.; Jackson, J. R.; DeWoody, A., 2010: Discovery and evaluation of candidate sex-determining genes and xenobiotics in the gonads of lake sturgeon (*Acipenser fulvescens*). Genetica **138**(7), 745–756.
- Harkness, W. J. K., 1923: The rate of growth and food of the lake sturgeon (*Acipenser rubicundus* Le Sueur). University of Toronto Studies, Biological Series 24. Publication of the Ontario Fisheries Research Laboratory 18.
- Harkness, W. J. K.; Dymond, J. R., 1961: The lake sturgeon the history of its fishery and problems of conservation. Fish and Wildlife Branch, Ontario Department of Lands and Forests, Canada, 121 pp.
- Haugen, G. N., 1969: Life history, habitat and distribution of the lake sturgeon, *Acipenser fulvescens*, in the South Saskatchewan River. Lands and Forests, Fish and Wildlife Division. Technical Document Res. Report No. 4. Dept., 27 pp.
- Haxton, T. J., 2003: Movement of lake sturgeon (*Acipenser ful-vescens*) in a natural reach of the Ottawa River. Can. Field Nat. 117, 541–545.
- Haxton, T. J., 2011: Depth selectivity and spatial distribution of juvenile lake sturgeon in a large fragmented river. J. Appl. Ichthyol. 27(Suppl. 2), 45–52.
- Haxton, T. J.; Findlay, C. S., 2008: Variation in lake sturgeon (Acipenser fulvescens) abundance and growth among river reaches in a large regulated river. Can. J. Fish Aquat. Sci. 65, 645–657.
- Haxton, T. J.; Findlay, C. S., 2009: Variation in large-bodied fishcommunity structure and abundance in relation to water-management regime in a large regulated river. J. Fish Biol. 74, 2216–2238.
- Haxton, T. J.; Findlay, C. S.; Threader, R. W., 2008: Predictive value of a lake sturgeon habitat suitability model. N. Am. J. Fish. Manage. 28(5), 1373–1383.
- Haxton, T. J.; Bruch, R. M.; Whelan, G., 2014a: Historical biomass and sustainable harvest of Great Lakes lake sturgeon (*Acipenser fulvescens* Rafinesque). J. Appl. Ichthyol. 30, 1371–1378.
- Haxton, T. J.; Friday, M.; Cano, T.; Hendry, C., 2014b: Variation in lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) abundance in rivers across Ontario, Canada. J. Appl. Ichthyol. 30, 1335–1341.
- Hay-Chmielewski, E. M., 1987: Habitat preferences and movement patterns of the lake sturgeon (*Acipenser fulvescens*) in Black lake, Michigan. Michigan Dept. of Natural Resources, Fisheries research Report No. 18, 51 pp.
- Hay-Chmielewski, L.; Whelan, G., 2003: Michigan Department of Natural Resources lake sturgeon rehabilitation strategy. Hay-Chmielewski, L. and Whelan, G. Fisheries Special Report No. 18. Lake Sturgeon Committee Report, 51 pp.
- Heinrich, T.; Friday, M., 2014: A Population Assessment of the Lake of the Woods – Rainy River Lake Sturgeon Population. Minnesota Department of Natural Resources, St. Paul, MN, USA, 38 pp.
- Hilton, E. J.; Bemis, W. E., 1999: Skeletal variation in shortnose sturgeon (*Acipenser brevirostrum*) from the Connecticut River:

- implications for comparative osteological studies of fossil and living fishes. In: Mesozoic Fishes II-Systematics and Fossil Record. G. Arratia, H. P. Schultze (Eds). Verlag Dr. Friedrich Pfeil Publishers, Munchen, Germany, pp. 69–94.
- Hochleitner, M.; Vecsei, P., 2004: Identification key to sturgeons and paddlefish of North America. In: Sturgeons and Paddlefish of North America. Fish and Fisheries Series. G. T. O. LeBreton, F. W. H. Beamish, R. S. McKinley (Eds). Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 315–318.
- Hoenig, J. M., 1983: Empirical use of longevity data to estimate mortality rates. Fish. B-NOAA 82(1), 898–903.
- Holey, M. E.; Baker, E. A.; Thuemler, T. F.; Elliot, R. F., 2000: Research and assessment needs to restore lake sturgeon in the Great Lakes – results of a workshop sponsored by the Great Lakes Fishery Trust. Great Lakes Fishery Trust, Lansing, MI, USA, 37 pp.
- Holtgren, J. M.; Auer, N. A., 2004: Movement and habitat of juvenile lake sturgeon (*Acipenser fulvescens*) in the Sturgeon River/ Portage Lake systems. J. Freshw. Ecol. 19, 419–432.
- Holzkamm, T.; McCarthy, M., 1988: Potential fishery for lake sturgeon (*Acipenser fulvescens*) as indicated by the returns of the Hudson's Bay Company Lac la Pluie District. Can. J. Fish Aquat. Sci. 45, 921–923.
- Homola, J. J.; Scribner, K. T.; Baker, E. A.; Auer, N. A., 2010: Genetic assessment of straying rates of wild and hatchery reared lake sturgeon (*Acipenser fulvescens*) in Lake Superior tributaries. J. Great Lakes Res. 36, 798–802.
- Homola, J. J.; Scribner, K. T.; Elliott, R. F.; Donofrio, M. C.; Kanefsky, J.; Smith, K. M.; McNair, J. N., 2012: Genetically derived estimates of contemporary natural straying rates and historical gene flow among Lake Michigan lake sturgeon populations. Trans. Am. Fish. Soc. 141, 1374–1388.
- Hoover, J. J.; Kilgore, K. J.; Clarke, D. G.; Smith, H.; Turnage, A.; Beard, J., 2005: Paddlefish and sturgeon entrainment by dredging: swimming performance as an indicator of risk. DOER Technical Note. U. S. Army Engineer Research and Development Center, Vicksburg, MS.
- Houston, J. J., 1987: Status of the lake sturgeon (Acipenser fulvescens) in Canada. Can. Field Nat. 101, 171–185.
- Hubbs, C. L.; Lagler, K. F., 1947: Fishes of the Great Lakes Region, Bulletin No. 26 ed. Cranbook Institute of Science, Bloomfield Hills, MI, USA, 186 pp.
- Humphries, P.; Lake, P. S., 2000: Fish larvae and the management of regulated rivers. Regul. River. 16, 421–432.
- Il'ina, L. K.; Gordeyev, N. A., 1972: Water-level regime and the spawning of fish stocks in reservoirs. J. Ichthyol. 12, 373–381.
- Jackson, J. R.; Van DeValk, A. J.; Brooking, T. E.; van Keeken, O. A.; Rudstrom, L. G., 2002: Growth and feeding dynamics of lake sturgeon, *Acipenser fulvescens*, in Oneida Lake, New York: results from the first five years of a restoration program. J. Appl. Ichthyol. 18, 439–443.
- Johnson, D. A.; Weisser, J. W.; Bills, T. D., 1999: Sensitivity of lake sturgeon (Acipenser fulvescens) to the lampricide 3-Trifluoromethyl-4-Nitrophenol (TFM) in laboratory and field exposures. Great Lakes Fishery Commission Technical Report 62, Ann Arbor, MI, 30 pp.
- Johnson, J. H.; LaPan, S. R.; Klindt, R. M.; Schiavone, A., 2006: Lake sturgeon spawning on artificial habitat in the St. Lawrence River. J. Appl. Ichthyol. 22, 465–470.
- Jollie, M., 1980: Development of head and pectoral girdle skeleton and scales in *Acipenser*. Copeia 1980, 226–249.
- Kampa, J.; Hatzenbeler, G.; Jennings, M., 2014: Status and management of lake sturgeon (*Acipenser fulvescens*) in the upper St. Croix River and Namekagon River, Wisconsin, USA. J. Appl. Ichthyol. 30, 1387–1392.
- Kempinger, J. J., 1988: Spawning and early life history of lake sturgeon in the Lake Winnebago system, Wisconsin. Am. Fish. Soc. Symp. 5, 111–122.
- Kempinger, J. J., 1996: Habitat, growth, and food of young lake sturgeons in the Lake Winnebago system, Wisconsin. N. Am. J. Fish. Manage. 15, 102–114.

- Kennedy, A. J.; Sutton, T. M., 2007: Effects of harvest and length limits on shovelnose sturgeon in the upper Wabash River, Indiana. J. Appl. Ichthyol. 23, 465–475.
- Kennedy, A. J.; Daugherty, D. J.; Sutton, T. M., 2007: Population characteristics of shovelnose sturgeon in the Upper Wabash River, Indiana. N. Am. J. Fish. Manage. 27, 52–62.
- Kerr, S. J., 2006: Lake Sturgeon. In S. Kerr (ed.), An historical review of fish culture, stocking and fish transfers in Ontario, 1865–2004. Fish & Wildlife Branch, Ontario Ministry of Natural Resources, Peterborough, ON, Canada, pp. 142–143.
- Kerr, S. J., 2011: Documentation of lake sturgeon habitat in the Ontario waters of the Great Lakes drainage basin. Biodiversity Branch, Ontario Ministry of Natural Resources, Peterborough, ON, Canada, 179 pp.
- Kerr, S. J.; Davison, M. J.; Funnell, E., 2011: A review of lake sturgeon habitat requirements and strategies to protect and enhance sturgeon habitat. Fisheries Policy Section, Biodiversity Branch, Ontario Ministry of Natural Resources, Peterborough, ON, Canada, 58 pp. + app.
- Killgore, K. J.; Hoover, J. J.; Kirk, J. P.; George, S. G.; Lewis, B. R.; Murphy, C. E., 2007: Age and growth of pallid sturgeon in the free-flowing Mississippi River. J. Appl. Ichthyol. 23, 452–456.
- Knights, B. C.; Vallazza, J. M.; Zigler, S. J.; Dewey, M. R., 2002: Habitat and movement of lake sturgeon in the upper Mississippi River system, USA. Trans. Am. Fish. Soc. 131, 507–522.
- Krieger, J.; Fuerst, P. A., 2004: Characterization of nuclear 18S rRNA gene sequence diversity and expression in an individual lake sturgeon (*Acipenser fulvescens*). J. Appl. Ichthyol. 20, 433– 439.
- Krieger, J.; Fuerst, P. A.; Cavender, T. M., 2000: Phylogenetic relationships of the North American sturgeons (Order Acipenseriformes) based on mitochondrial DNA sequences. Mol. Phylogenet. Evol. 16, 64–72.
- Krykhtin, M. L., 1986: Rate of sexual maturity and reproductive rhythm of Kaluga sturgeon *Huso dauricus* (Georgi) in the Amur Liman. J. Ichthyol. 29(1), 66–75.
- de Lafontaine, Y.; Costan, G., 2002: Introduction and transfer of alien aquatic species in the Great Lakes-St. Lawrence River drainage basin. In: Alien invaders in Canada's waters, wetlands, and forests. R. Claudi, P. Nantel, E. Mickle-Jeffs (Eds). Canadian Forest Services, Ottawa, ON, Canada, 320 pp.
- LaHaye, M., 1982: Comparison de la biologie et de l'ecologie des jeunes stades de l'esturgeon jaune (*Acipenser fulvescens*) dans les rivières des Prairies et L'Assomption. près de Montréal Mémoire présenté comme exigence partielle de la Maîtrise en Sciences de l'Environnement. Université du Québec á Montréal, Canada, 135 pp.
- LaHaye, M.; Fortin, R., 1990: Caractérisation de l'habitat de fraie et de l'habitat des juvéniles de l'esturgeon jaune (*Acipenser ful-vescens*) dans la région de Montréal. Département des sciences biologiques, Université du Québec á Montréal, Canada, 81 pp. + app.
- LaHaye, M.; Branchaud, A.; Gendron, M.; Verdon, R.; Fortin, R., 1992: Reproduction, early life history, and characteristics of the spawning grounds of the lake sturgeon (*Acipenser fulvescens*) in Des Prairies and L'Assomption rivers, near Montreal, Quebec. Can. J. Zool. 70, 1681–1689.
- Lallaman, J. J.; Damstra, R. A.; Galarowicz, T. L., 2008: Population assessment and movement patterns of lake sturgeon (*Acipenser fulvescens*) in the Manistee River, Michigan, USA. J. Appl. Ichthyol. 24, 1–6.
- Lane, J. A.; Portt, C. B.; Minns, C. K., 1996: Nursery habitat characteristics of Great Lakes fishes. Canadian Manuscript Report of Fisheries and Aquatic Sciences No. 2338, 44 pp.
- LeBreton, G. T. O.; Beamish, F. W. H., 1998: The influence of salinity on ionic concentrations and osmolarity of blood serum in lake sturgeon, *Acipenser fulvescens*. Environ. Biol. Fish. 52, 477–482.

- Lenhardt, M.; Jaric, I.; Kalauzi, A.; Cvijanovic, G., 2006: Assessment of extinction risk and reasons for decline in sturgeon. Biodivers. Conserv. 15, 1967–1976.
- Linton, B. C.; Hansen, M. J.; Schram, S. T.; Sitar, S. P., 2007: Dynamics of a recovering lake trout population in eastern Wisconsin waters of lake Superior, 1980–2001. N. Am. J. Fish. Manage. 27, 940–954.
- Liu, J. K.; Yu, Z. T., 1992: Water quality changes and effects on fish populations in the Hanjiang River, China, following hydroelectric dam construction. Regul. River. 7, 359–368.
- Lord, K., 2007: Movements and habitat use of juvenile lake sturgeon in the North Channel of the St. Clair River. MSc Thesis. University of Michigan, Ann Arbor, MI, 39 pp.
- Lowie, C.; Hughes, T.; Schlueter, S., 2000: Great Lakes Native Fish Restoration: Lake Sturgeon, FY 1997 Fisheries Stewardship Proposal Final Progress Report. USFWS Region 5 Report, 23 pp.
- Ludwig, A.; Belfiore, N. M.; Pitra, C.; Svirsky, V.; Jenneckens, I., 2001: Genome duplication events and functional reduction of ploidy levels in sturgeon (*Acipenser*, *Huso* and *Scaphirhynchus*). Genetics 158, 1203–1215.
- Magnin, E., 1966: Coissance de l'esturgeon *Acipenser fulvescens* Raf. Vivant dans le basin hydrographique de la riviére Nottaway, tributaire de la baie James. Nat. Can. **92**, 193–204.
- Magnin, E., 1977: Croissance, régime alimentaire, et fécondité des esturgeons, Acipenser fulvescens, du basin hydrographique de la Grand Riviére (Québec). Nat. Can. 104, 419–427.
- Magnin, E.; Harper, P. P., 1970: La nourriture des esturgeons, Acipenser fulvescens de la riviére Nottaway, tributaire de la Baie James. Nat. Can. 97, 73–85.
- Mailhot, Y.; Dumont, P.; Vachon, N., 2011: Management of the Lake Sturgeon Acipenser fulvescens population in the lower St Lawrence River (Québec, Canada) from the 1910s to the present. J. Appl. Ichthyol. 27(2), 405–410.
- Manitoba, 2012.; Manitoba Conservation and Water Stewardship Branch. (Online at: http://fw.ky.gov/Fish/Pages/Lake-Sturgeon.aspx)
- Manitoba Hydro, 2014: Lake Sturgeon in Manitoba, a summary of current knowledge. Winnipeg, MN, Canada, 48 pp.
- Manny, B. A.; Kennedy, G. W., 2002: Known lake sturgeon (Acipenser fulvescens) spawning habitat in the channel between lakes Huron and Erie in the Laurentian Great Lakes. J. Appl. Ichthyol. 18, 486–490.
- Marranca, J. M.; Welsh, A. B.; Roseman, E., 2015: Genetic effects of habitat restoration in the Laurentian Great Lakes: an assessment of lake sturgeon origin and genetic diversity. Restor. Ecol. 23 455-464
- McCabe, D. J.; Beekey, M. A.; Mazloff, A.; Marsden, J. E., 2006: Negative effect of zebra mussels on foraging and habitat use by lake sturgeon (*Acipenser fulvescens*). Aquat. Conserv. 16, 493– 500.
- McCormick, C. R.; Bos, D. H.; DeWoody, J. A., 2008: Multiple molecular approaches yield no evidence for sex-determining genes in lake sturgeon (*Acipenser fulvescens*). J. Appl. Ichthyol. 24, 643–645.
- McDermid, J. L.; Wozney, K. M.; Kjartanson, S. L.; Wilson, C. C., 2011: Quantifying historical, contemporary, and anthropogenic influences on the genetic structure and diversity of lake sturgeon (*Acipenser fulvescens*) populations in northern Ontario. J. Appl. Ichthyol. 27, 12–23.
- McDonald, D., 1998: Nelson River sturgeon studies: five-year report to the Nelson River Sturgeon Co-Management Board. Manitoba Department of Natural Resources, Fisheries Branch, Winnipeg, MN, Canada, 44 pp.
- McDougall, C. A.; Blanchfield, P. J.; Peake, S. J.; Anderson, W. G., 2013: Movement patterns and size-class influence entrainment susceptibility of lake sturgeon in a small hydroelectric reservoir. Trans. Am. Fish. Soc. 142, 1508–1521.
- McDougall, C. A.; Anderson, W. G.; Peake, S. J., 2014: Down-stream passage of lake sturgeon through a hydroelectric

generating station: route determination, survival, and fine-scale movement. N. Am. J. Fish. Manage. **34**, 546–558.

- McKinley, R. S.; Singer, T. D.; Ballantyne, J. S.; Power, G., 1993: Seasonal variation in plasma nonesterified fatty acids of lake sturgeon (*Acipenser fulvescens*) in the vicinity of hydroelectric facilities. Can. J. Fish Aquat. Sci. **50**, 2440–2447.
- McKinley, S.; Van Der Kraak, G.; Power, G., 1998: Seasonal migrations and reproductive patterns in the lake sturgeon (*Acipenser fulvescens*) in the vicinity of hydroelectric stations in northern Ontario. Environ. Biol. Fish. **51**, 245–256.
- McQuown, E. C.; Gall, G. A. E.; May, B., 2002: Characterization and inheritance of six microsatellite loci in lake sturgeon. Trans. Am. Fish. Soc. 131, 299–307.
- McQuown, E. C.; Krueger, C. C.; Kincaid, H. L.; Gall, G. A. E.; May, B., 2003: Genetic comparison of lake sturgeon populations: differentiation based on allelic frequencies at seven microsatellite loci. J. Great Lakes Res. 29, 3–13.
- Mirza, M. Q.; Ericksen, N. J., 1996: Impact of water control projects on fisheries resources in Bangladesh. Environ. Manage. 20, 523– 539.
- Morse, S. D.; Weaver, H. T.; Linder, A. T.; Hugill, R. A., 1997: Habitat Suitability Curves For Lake Sturgeon Based On Radio-Telemetry Observations In The Kettle River, Minnesota. Mn. Dept. Nat. Res. Completion Rept., Proj. F-29-R(P), Area 330, Study 4, Job 448, 48 pp.
- Mosindy, T. E.; Rusak, J., 1991: An assessment of the lake sturgeon population in Lake of the Woods and Rainy River. Lake of the Woods Fisheries Assessment Unit Report 1991-01. Ontario Ministry of Natural Resources, Kenora, ON, Canada, 66 pp.
- Nevin, J., 1919: Sturgeon in Wisconsin waters. The Wisconsin Conservationist Vol 1, March 1919.
- Nicols, S. J.; Kennedy, G.; Crawford, E.; Allen, J.; French, J., III; Black, G.; Blouin, M.; Hickey, J.; Chernyák, S.; Haas, R.; Thomas, M., 2003: Assessment of lake sturgeon (*Acipenser ful-vescens*) spawning efforts in the lower St. Clair River, Michigan. J. Great Lakes Res. 29, 383–391.
- Nilo, P., 1996: Year class strength, habitat, and feeding of juvenile lake sturgeon (*Acipenser fulvescens*) in the St. Lawrence system. MSc Thesis. University of Québec, Montréal, QC.
- Nilo, P.; Tremblay, S.; Bolon, A.; Dodson, J.; Dumont, P.; Fortin, R., 2006: Feeding ecology of juvenile lake sturgeon in the St. Lawrence River system. Trans. Am. Fish. Soc. 135, 1044–1055.
- Nilsson, C.; Berggren, K., 2000: Alterations of riparian ecosystems caused by river regulation. Bioscience **50**, 783–792.
- Nilsson, C.; Reidy, C. A.; Dynesius, M.; Revenga, C., 2005: Fragmentation and flow regulation of the world's large river systems. Science 308, 405–408.
- Nowak, A. M.; Jessop, C. S., 1987: Biology and management of the lake sturgeon (*Acipenser fulvescens*) in the Groundhog and Mattagami rivers, Ontario. In: Proceedings of a Workshop on the Lake Sturgeon (*Acipenser fulvescens*). Ed. C.H. Olver. Ont. Fish. Tech. Rep. Ser. No. 23, Ontario Ministry of Natural Resources, Toronto, ON, Canada, pp. 20–32.
- Ontario Ministry of Natural Resources, 2009: The lake sturgeon in Ontario. Fish and Wildlife Branch. Peterborough, Ontario, 48 pp. + app.
- Paragamian, V. L.; Beamesderfer, R. C. P., 2003: Growth estimates from tagged white sturgeon suggest that ages from fin rays underestimate true age in the Kootenai River, USA and Canada. Trans. Am. Fish. Soc. 132, 895–903.
- Paragamian, V. L.; Beamesderfer, R. C. P., 2004: Dilemma on the Kootenai River – the risk of extinction or when does the hatchery become the best option? Am. Fish. Soc. Symp. 44, 377–385.
- Paragamian, V. L.; Hansen, M. J., 2008: Evaluation of recovery goals for endangered white sturgeon in the Kootenai River, Idaho. N. Am. J. Fish. Manage. 28, 463–470.
- Paragamian, V. L.; Beamesderfer, R. C. P.; Ireland, S. C., 2005: Status, population dynamics, and future prospects of the

- endangered Kootenai white sturgeon population with and without hatchery intervention. Trans. Am. Fish. Soc. **134**, 518–532.
- Patrick, H. K.; Sutton, T. M.; Swink, W. D., 2009: Lethality of sea lamprey parasitism on lake sturgeon. Trans. Am. Fish. Soc., 138 (5), 1065–1075.
- Pauly, D., 1980: On the interrelationships between natural mortality, growth parameters, and mean environmental temperatures in 175 fish stocks. J. Cons. Int. Explor. de la Mer 39, 175–192.
- Peake, S., 1999: Substrate preferences of juvenile hatchery-reared lake sturgeon (*Acipenser fulvescens*). Environ. Biol. Fish. **56**, 367–374.
- Peterson, D. L.; Vecsei, P.; Noakes, D. L. G., 2003: Threatened fishes of the world: *Acipenser fulvescens* Rafinesque, 1817 (Acipenseridae). Environ. Biol. Fish. **68**, 174.
- Peterson, D. L.; Vecsei, P.; Jennings, C., 2007: Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Rev. Fish Biol. Fisher. 17, 59–76.
- Pianka, E. R., 1970: On r- and K-selection. Am. Nat. 104, 592–597.
  Pikitch, E. K.; Doukakis, P.; Lauck, L.; Chakrabarty, P.; Erickson, D. L., 2005: Status, trends and management of sturgeon and paddlefish fisheries. Fish Fish. 6, 233–265.
- Pine, W. E.; Allen, M. S.; Dreitz, V. J., 2001: Population viability of the Gulf of Mexico Sturgeons: inferences from Capture-Recapture and Age Structured Models. Trans. Am. Fish. Soc. 130, 1164–1174.
- Priegel, G. R., 1973: Lake sturgeon management on the Menominee River. Wisconsin Department of Natural Resources Technical Bulletin Number 67, 20 pp.
- Priegel, G. R.; Wirth, T. L., 1971: The lake sturgeon; its life history, ecology and management. Wisconsin Department of Natural Resources Publication 240-70, 19 pp.
- Priegel, G. R.; Wirth, T. L., 1975: Lake sturgeon harvest, growth and recruitment in Lake Winnebago, Wisconsin. Wisconsin Department of Natural Resources Technical Bulletin 83. Madison, WI, USA, 25 pp.
- Prince, E. E., 1905: The Canadian Sturgeon and Caviare Industries. Sessional Paper. Volume 9. First Session of the Tenth Parliament of the Dominion of Canada. Volume XXXIX.
- Pringle, C. M.; Freeman, M. C.; Freeman, B. J., 2000: Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons. Bioscience 50, 807–823.
- Probst, R. T., 1954: Why study sturgeon. Wisconsin Conserv. Bull., 19(3), 3-5.
- Probst, R. T.; Cooper, E. L., 1954: Age, growth, and production of the lake sturgeon (*Acipenser fulvescens*) in the Lake Winnebago region, Wisconsin. Trans. Am. Fish. Soc. 84, 207–227.
- Pyatskowit, J. D.; Krueger, C. C.; Kincaid, H. L.; May, B., 2001: Inheritance of microsatellite loci in the polyploid lake sturgeon (Acipenser fulvescens). Genome 44, 185–191.
- Quist, M. C.; Guy, C. S.; Pegg, M. A.; Braaten, P. J.; Pierce, C. L.; Travnichek, V. H., 2002: Potential influence of harvest on shovelnose sturgeon populations in the Missouri River System. N. Am. J. Fish. Manage. 22, 537–549.
- Raikova, E. V., 1994: Life cycle, cytology, and morphology of *Polypodium hydriforme*, a coelenterate parasite of the eggs of acipenseriform fishes. J. Parasitol., **80**(1), 1–22.
- Randall, R. G., 2008: Narrative description and quantification of the habitat requirements of lake sturgeon (*Acipenser fulvescens*) in the Great Lakes and upper St. Lawrence River. Research Document, Department of Fisheries and Oceans, Burlington, ON, Canada, 16 pp.
- Richter, V. A.; Efanov, V. N., 1976: On one of the approaches to estimation of natural mortality of fish populations. International Commission of Northwest Atlantic Fisheries Research Document 79/VI/8, 12 pp.
- Ricker, W. E., 1975: Computation and interpretation of biological statistics of fish populations. Fisheries Research Board Canada Bulletin, 191, 382 pp.

- Rien, T. A.; Beamesderfer, R. C., 1994: Accuracy and precision of white sturgeon age estimates from pectoral fin rays. Trans. Am. Fish. Soc. 123(2), 255–265.
- Rochard, E.; Castelnaud, G.; LePage, M., 1990: Sturgeon (Pisces: Acipenseridae); threats and prospects. J. Fish Biol. 37, 123-132.
- Roseman, E. F.; Manny, B. A.; Boase, J.; Child, M.; Kennedy, G.; Soper, K.; Drouin, R., 2011: Lake sturgeon response to a spawning reef constructed in the Detroit River. J. Appl. Ichthyol. 28(Suppl. 2), 66–76.
- Rossiter, A.; Noakes, D. L. G.; Beamish, E. W. H., 1995: Validation of age estimation for the lake sturgeon. Trans. Am. Fish. Soc. 124, 777–781.
- Royer, L. M.; Atton, F. M.; Cuerrier, J. P., 1968: Age and growth of lake sturgeon in the Saskatchewan River delta. J. Fish. Res. Bd. Can. 25, 1511–1516.
- Rusak, J. A.; Mosindy, T., 1997: Seasonal movements of lake sturgeon in Lake of the Woods and the Rainy River, Ontario. Can. J. Zool. 74, 383–395.
- Sandilands, A. P., 1987: Biology of the lake sturgeon (*Acipenser fulvescens*) in the Kenogami River, Ontario. In: Proceedings of a workshop on the lake sturgeon (*Acipenser fulvescens*). Ontario Fisheries Technical Report Series No. 23. Ontario Ministry of Natural Resources, 99 pp.
- Schneberger, E.; Woodbury, L. A., 1946: The lake sturgeon, *Acipenser fulvescens* Rafinesque, in Lake Winnebago, Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. **36**, 131–140.
- Scholl, D. K., 1986: Lake sturgeon of the upper North Fork Flambeau River. Wisconsin Department of Natural Resources internal fish management report, Mercer, WI, USA, 21 pp.
- Scott, W. B.; Crossman, E. J., 1973: Freshwater Fishes of Canada. Bull. Fish. Res. Bard Can., 184, XI, 966 pp.
- Seyler, J., 1997: Biology of selected riverine fish species in the Moose River basin. Ontario Min. Nat. Res. NEST Information Report IR-024. South Porcupine, ON, Canada, 100 pp.
- Seyler, J.; Evers, J.; McKinley, S.; Evans, R.; Prevost, G.; Carson, R.; Phoenix, D., 1996: Mattagami River lake sturgeon entrainment: Little Long generating station facilities. TR-031.
  Timmins, Queen's Printer for Ontario. NEST Technical Report.
- Shaw, S. L.; Chipps, S. R.; Windels, S. K.; Webb, M. A. H.; McLeod, D. T., 2013: Influence of sex and reproductive status on seasonal movements of lake sturgeon in Namakan Reservoir, Minnesota-Ontario. Trans. Am. Fish. Soc. 142, 10–20.
- Sheehan, R., 2001: Adam Creek Lake Sturgeon relocation program review 1990–2000. R-FJ20-07015.01-0001, -67. Environment Electrical Production.
- Singer, T. D.; Mahadevappa, V. G.; Ballantyne, J. S., 1990: Aspects of the energy metabolism of lake sturgeon, *Acipenser fulvescens*, with special emphasis on lipid and ketone body metabolism. Can. J. Fish Aquat. Sci. 47, 873–881.
- Smith, K. M., 2003: Spawning stock abundance and larval production of lake sturgeon (Acipenser fulvescens) in Black Lake, Michigan. MSc Thesis. Central Michigan University.
- Smith, K. M.; Baker, E. A., 2005: Characteristics of spawning lake sturgeon in the upper Black River, Michigan. N. Am. J. Fish. Manage. 25, 301–307.
- Smith, A. L.; Hobden, D., 2011: A synopsis of lake sturgeon (Acipenser fulvescens) culture, marking, and stocking techniques. Biodiversity Branch. Ontario Ministry of Natural Resources, Peterborough, ON, Canada, 36 pp.
- Smith, K. A.; King, D. K., 2005a: Dynamics and extent of larval lake sturgeon *Acipenser fulvescens* drift in the Upper Black River, Michigan. J. Appl. Ichthyol. 21, 161–168.
- Smith, K. A.; King, D. K., 2005b: Movement and habitat use of yearling and juvenile lake sturgeon in Black Lake, Michigan. Trans. Am. Fish. Soc. 134, 1159–1172.
- Smith, A.; Smokorowski, K.; Marty, J.; Power, M., 2016: Stable isotope characterization of Rainy River, Ontario, lake sturgeon diet and trophic position. J. Great Lakes Res., 42, 440– 447.

- Stelzer, R. S.; Drecktrah, H. G.; Schupryt, M. P.; Bruch, R. M., 2008: Carbon sources for lake sturgeon (*Acipenser fulvescens*) in Lake Winnebago, WI. Trans. Am. Fish. Soc. 137, 1018–1028.
- Sunde, L. A., 1961: Growth and reproduction of the lake sturgeon (*Acipenser fulvescens* Rafinesque) of the Nelson River in Manitoba. MSc Thesis. University of British Columbia, 93 pp.
- Taghavi, M. A., 2001: An estimation of growth parameter, mortality rates and yield per recruit for Beluga (*Huso huso*) living in the Caspian Sea. Iran. J. Fish. Sci. 3(2), 25–48.
- Talmage, P.; Heinrich, T.; Topp, d., Peterson, K., , 2009: Objectives and Strategies for Lake Sturgeon Management for Lake of the Woods & Rainy River. MN Dept. Nat. Res, Management Report, Baudette, MN, USA. 16 pp.
- Thomas, M. V.; Haas, R. C., 2001: Abundance, age structure, and spatial distribution of lake sturgeon *Acipenser fulvescens* in the St. Claire System. Michigan Department of Natural Resources, Fisheries Research Report 2076, 27 pp.
- Threader, R. W.; Brousseau, C. S., 1986: Biology and management of the lake sturgeon in the Moose River, Ontario. N. Am. J. Fish. Manage. 6, 383–390.
- Threader, R. W.; Pope, R. J.; Schaap, P. R. H., 1998: Development of a habitat suitability index model for lake sturgeon (*Acipenser fulvescens*). Report prepared for Ontario Hydro. Toronto, ON, Canada, Report H-07015.01-0012.
- Thuemler, T. F., 1997: Lake sturgeon management in the Menominee River, a Wisconsin-Michigan boundary water. Environ. Biol. Fish. 48, 311–317.
- Tody, W. H., 1974: Whitefish, sturgeon, and the early Michigan commercial fishery. Michigan Fisheries Centennial Report 1873– 1973. Michigan Department of Natural Resources, Lansing, MI, Canada, pp. 45–60.
- Towns, G. L.; Thomas, M. V., 2011: Michigan's St. Clair System Lake Sturgeon Fishery: Results of an Angler Postal Survey. MI Dept. Nat. Res. Tech. Rept. 2011–2, Lansing, MI, USA. 20 pp.
- Trested, D. G.; Chan, M. D.; Bridges, W. C.; Isely, J. J., 2011: Seasonal movement and mesohabitat usage of adult and juvenile lake sturgeon in the Grasse River, New York. Trans. Am. Fish. Soc. 140, 1006–1014.
- Van Eenenaam, J. P.; Doroshov, S. I.; Moberg, G. P.; Watson, J. G.; Moore, D. S.; Linares, J., 1996: Reproductive conditions of the Atlantic sturgeon (*Acipenser oxyrinchus*) in the Hudson River. Estuaries, 19(4), 769–777.
- Vecsei, P.; Peterson, D. L., 2004: Sturgeon ecomorphology: a descriptive approach. In: Sturgeons and Paddlefish of North America. G. T. O. LeBreton, F. W. H. Beamish, R. S. McKinley (Eds). Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 103–133.
- Veshchev, P. V., 1981: Effect of dredging operations in the Volga River on migration of sturgeon larvae. J. Ichthyol. 21, 108-117.
- Vladykov, V. D.; Greeley, J. R., 1963: Order Acipenseroidei. In: Fishes of the Western North Atlantic, Part Three. H. B. Bigelow, C. M. Breeder, D. M. Cohen, G. W. Mead, D. Merriman, Y. H. Olsen, W. C. Schroeder, L. P. Schultz, L. Teevan (Eds). Sears Foundation for Marine Research, Yale University, New Haven, CT, USA, pp. 24–60.
- WDNR, 2000: Lake Sturgeon Management Plan. Bureau of Fisheries Management. Madison, WI, USA, 16 pp.
- Welsh, A.; May, B., 2006: Development and standardization of disomic microsatellite markers for lake sturgeon genetic studies. J. Appl. Ichthyol. 22, 337–344.
- Welsh, A.; McLeod, D., 2010: Detection of natural barriers to lake sturgeon (*Acipenser fulvescens*) movement within the Namakan River, Ontario. Can. J. Zool. 88, 390–397.
- Welsh, A. B.; Blumberg, M.; May, B., 2003: Identification of microsatellite loci in lake sturgeon, *Acipenser fulvescens*, and their variability in green sturgeon, *A. medirostris*. Mol. Ecol. Notes 3, 47–55.
- Welsh, A.; Hill, T.; Quinlan, H.; Robinson, C.; May, B., 2008: Genetic assessment of lake sturgeon population structure in the

Laurentian Great Lakes. N. Am. J. Fish. Manage. 28, 572-591.

- Wilberg, M. J.; Bence, J. R.; Eggold, B. T.; Makaukas, D.; Clapp, D., 2005: Yellow perch dynamics in Southwestern Lake Michigan during 1986-2002. N. Am. J. Fish. Manage. 25, 1130–1152.
- Williot, P.; Arlati, G.; Chebanov, M.; Gulyas, T.; Kasimov, R.; Kirschbaum, F.; Patriche, N.; Pavlovskaya, L. P.; Poliakova, L.; Pourkazemi, M.; Kim, Y.; Zhuang, P.; Zholdasova, I. M., 2002: Status and management of Eurasian sturgeon: an overview. Int. Rev. Hydrobiol. 87, 483–506.
- Wilson, J. A.; McKinley, R. S., 2004: Distribution, Habitat, and Movements. In: Sturgeons and Paddlefish of North America. G. LeBreton, F. Beamish, S. McKinley (Eds). Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 40– 72
- Winemiller, K. O.; Rose, K. A., 1992: Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish Aquat. Sci. 9, 2196–2218.

- Wishingrad, V.; Carr, M. K.; Pollock, M. S.; Ferrari, M. C. O.; Chivers, D. P., 2014: Lake sturgeon geographic range, distribution, and migration patterns in the Saskatchewan River. Trans. Am. Fish. Soc. 143, 1555–1561.
- Woodland, R. J., 2005: Age, growth, and recruitment of Hudson River shortnose sturgeon (*Acipenser brevirostrum*). MSc Thesis. University of Maryland, College Park, MD, 117 pp.
- Woodland, R. J.; Secor, D. H., 2007: Year class strength and recovery of endangered shortnose sturgeon in the Hudson River, New York. Trans. Am. Fish. Soc. 136, 72–81.
- Zhong, Y.; Power, G., 1996: Environmental impacts of hydroelectric projects on fish resources in China. Regul. River. 12, 81–98.
- Zimmerman, G. S.; Horton, R. R.; Dessecker, D. R., 2008: New insight to old hypotheses: ruffed grouse population cycles. Wilson J. Ornithol. **120**(2), 239–247.
- Author's address: Ronald M. Bruch, Wisconsin Department of Natural Resources (retired), 818 Hennessy St., Oshkosh, Wisconsin, USA.

E-mail: ronaldmbruch@gmail.com